ARTICLES



The Case for Welfare Biology

Asher A. Soryl¹ · Andrew J. Moore² · Philip J. Seddon³ · Mike R. King¹

Accepted: 3 March 2021 / Published online: 15 March 2021 © The Author(s), under exclusive licence to Springer Nature B.V. 2021

Abstract

Animal welfare science and ecology are both generally concerned with the lives of animals, however they differ in their objectives and scope; the former studies the welfare of animals considered 'domestic' and under the domain of humans, while the latter studies wild animals with respect to ecological processes. Each of these approaches addresses certain aspects of the lives of animals living in the world though neither, we argue, tells us important information about the welfare of wild animals. This paper argues for the development of a new scientific discipline 'welfare biology' to address these issues and more, given the deficiencies of pre-existing life science disciplines to research the subject. Welfare biology is the study of the welfare of all living beings who have a welfare, with a value orientation toward promoting that welfare, regardless of the beings' situation or relationship to humans and our activities.

Keywords Welfare · Wild animals · Animal welfare · Animal welfare science · Ecology · Wild animal suffering · Animal ethics · Non-speciesism

Introduction

Nonhuman animal (hereafter 'animal') welfare has been treated as an important cause by scientists, legislators, and philosophers for hundreds—and even thousands—of years (Blosh, 2012; Salt, 1894). Such figures recognise that many different animals (in addition to humans) have a welfare that is morally considerable or gives rise to their moral consideration as individuals. The concept of welfare is also valuable to understand and know about (that is to say it has epistemic value), and there are many different reasonable perspectives on what makes one's life go better

Mike R. King mike.king@otago.ac.nz

¹ Bioethics Centre, Dunedin School of Medicine, University of Otago, Dunedin, New Zealand

² Department of Philosophy, University of Otago, Dunedin, New Zealand

³ Department of Zoology, University of Otago, Dunedin, New Zealand

or worse for oneself. We do not argue for the ethical value of welfare in this paper, but rather proceed on the basis that, insofar as one accepts these positions, we have good reasons to learn more about and promote welfare wherever it is present.

In this paper, we focus on the welfare of wild animals independent of human activities as an area of research that has been neglected in both respects: we do not know enough about it, nor do enough to advance it, given the broad acceptance of its value. The general condition of wild animals with respect to their welfare is yet unknown, and our understanding of the ecological dynamics of welfare is mostly speculative. Pre-existing fields such as animal welfare science and ecology might individually address some aspects of wild animal welfare, however we argue that neither is sufficient to address the problem of widespread wild animal suffering (hereafter, 'WWAS') which lacks an established empirical foundation. Rather than continuing to expand these fields, we advocate for the development of a new scientific discipline 'welfare biology'.

In addition to this problem, welfare biology is also concerned with identifying subjects of welfare which in this paper we assume to include all sentient beings. To be sentient is to have the capacity for positive and negative mental states (such as pleasure and pain). We proceed in our discussion about wild animal welfare on the plausible assumption that any being that is sentient has a welfare: they can be benefited or harmed, their life go well or badly for them. This does not mean that *only* sentient beings have a welfare; rather, it is a useful marker to identify at least *some* plausible subjects whose welfare we currently know very little about— namely, sentient wild animals, which may include fish and invertebrates.

Our argument is laid out as follows. First, we describe the divergent development of animal ethics and welfare science to give context to their differential consideration of animal welfare. This includes differences in consideration for wild animals, a group which have traditionally been the focus of studies in ecology and conservation under the assumption that natural ecosystems provide for their welfare. We then introduce the WWAS concept in detail, describing how conditions in nature may plausibly result in more negative welfare than positive welfare to occur in the lives of most individuals who come into existence. The issue of uncertainty about sentience (which we regard as a sufficient property for an animal to be a subject of welfare) adds another layer to the problem we present, given the demographics of most wild animals and the dearth of research analysing the possible welfare of nonmammals. To respond to these issues, we return to consider the potential suitability of welfare science and ecology as pre-existing disciplines, which we reject in favour of establishing welfare biology.

Animal Ethics in the Sciences

Animal ethics is a study field which analyses the relationship between humans and nonhuman animals and considers their standing in relation to moral decision making. Underlying this field is a set of normative postulates that both values the status of certain animals—for example, as sentient beings or 'subjects of life'—and condemns speciesism, which is the unjustified discriminatory consideration or treatment between individuals because of their species classification (rather than a difference of morally relevant properties) (Degrazia, 1999, p. 112, Horta, 2010a, p. 5). Traditional animal ethics has focussed on the intrinsic value of animals, and the moral respect and treatment they are due by moral agents because of this, including their liberation from use as resources, and promotion of their welfare.¹

In contrast, the advancement of animal welfare within the biological sciences has taken a more conservative approach to formulating and applying concepts of welfare to animals (Bekoff & Pierce, 2017, p. 24). Rather than condemning on moral principle practices that involve harmful, or potentially wrongful, human use of animals (such as some agriculture, biomedical research, or use in entertainment), as generally considered the norm in the animal ethics orthodoxy, the position adopted by most welfare scientists was (and remains) more directed toward cooperation with industries that engage in such practices to improve welfare. This corresponds to the circumstances of welfare science's inception as the field was born out of a political process initiated in response to public concern about animal husbandry conditions, rather than a conceptual interest in the abolition of such practices altogether (Fraser, 2008, pp. 62–63, Broom, 2011, p. 124). In the years following its initial emergence, welfare science has founded itself in a variety of other fields both within and outside of the life sciences (Mellor et al. 2009, p. 187).

Despite their common genesis in the late 1960s, methodological differences between philosophical and scientific perspectives on animal welfare created a division that to date remains unresolved, creating conflict in the application of their research (Fraser, 1999, p. 173). This dispute suggests that animal ethics and welfare science are not so close as one might initially anticipate given their common concern about animal welfare, which gives context to some of their disagreements and limited collaboration. However, an important commonality to note between the two fields is that they each accept and endorse the notion that many animals are sentient (meaning that they have the capacity to experience conscious states of affect, such as pain).²

While this view is considered standard under the current paradigm of animal research, for the greater part of history this has not always been the case and the scientific study of mental states in animals is a fairly recent research tradition. Broadly speaking, the success of behaviourism in the twentieth century set back scientific consideration of animal mental capacities and states significantly. The advent of welfare science and the rejuvenation of animal ethics in the later twentieth century contributed to a shift away from the proscriptions of behaviourism, as did the

¹ Different conceptions of welfare may change *how* animals are considered within a given normative theory – for example, bodily health and integrity might be considered objective goods in animals because of their intrinsic value, or instrumental toward other ends such as the reduction of unnecessary suffering or frustration of preferences (Nussbaum 2006, pp. 394–395). The aim of this paper is not to discriminate between these positions, so we assume that general markers of good and bad welfare are morally important.

² Exactly *which* animals are considered sentient and for what reasons we shall address in a later section.

research of Donald Griffin who founded the field of cognitive ethology (Jamieson & Bekoff, 1990, p. 156).³

These developments mark the acceptance of mentalistic research concerning animals in the sciences. However, this does not imply a complete revolution in the attitudes of all those whose research concerned animals. The disruptive presence of behaviourism on the perceived legitimacy of mentalistic research has resulted in many present-day fields (such as welfare science) being underdeveloped relative to their peers. Many still note lingering after-effects which manifest as a reluctance for researchers to consider the role of affective states within animal psychological concepts and the concept of welfare, and a more general scepticism about the value of such states while they are being researched (Fraser, 1999, p. 173, Dawkins, 2017, p. 4, Rollin, 2019, p. 9).⁴

By describing these challenges presented over the course of welfare science's development, we hope to give context to its divergence from animal ethics, a field which developed without such paradigmal constraints. Both fields are broadly concerned with promoting the welfare of animals, yet their aims and attitudes differ significantly such that the questions and topics each field addresses are, or have been in the past, difficult to reconcile. Welfare scientists, for instance, tend emphasise refrain from harming animals when they are under human control, rather than seeking to reduce harm because of its inherent disvalue in all situations in which it might occur (Faria, 2016a, pp. xiv–xv, Moen, 2016, p. 91).⁵⁶ Animal welfare is thus considered important insofar as it is under direct threat from human activity. Many animal ethicists hold this position also, though it is more common to recognise the inherent value of animals as sentient beings which exists independent of their actual or counterfactual relations with humans. These views have relevance to the welfare of wild animals, which we shall now discuss.

³ Cognitive ethology is sometimes mistaken for the pre-existing field of comparative animal psychology given their shared objectives in understanding the contents of animal minds. Major differences between the two relate to their conceptual orientations; cognitive ethologists tend to *assume* the presence of consciousness in their account of animal cognition, while it is common for comparative psychologists to limit their discussion of mentalistic events. Other differences include experimental variation, research methodology, and limitations that scientists working in these fields might expect to encounter (Vauclair 1997, pp. 36–38, Allen and Bekoff 2007, p. 309).

⁴ Associated with the positivist view that the inclusion of non-epistemic values threatens 'good science' by increasing inductive risk (the risk of error in accepting or rejecting scientific hypotheses), expressed by Hempel and many others (Douglas2000, p. 561).

⁵ e.g., large farm mammals are generally given much greater priority than other animal groups in the discussion of our ethical obligations toward animals (Walker et al. 2014, p. 86). Note, however, that in recent years farmed fish have increasingly been studied with reference to welfare concepts (Lund et al. 2007, Walker et al. 2014, p. 90).

⁶ Held in addition to the common intuition that doing harm is ethically worse than allowing harm to occur.

Wildlife Ethics

Because animals are subjects of moral concern, many animal ethicists accept that promoting their welfare is something that is worth doing for its own sake (or at least, that it is permissible to do so). Most accept a version of this argument when considering dire circumstances under which members of our own species suffer—say, resulting from hunger or malnourishment. Some even argue that we can have duties or obligations of assistance to prevent such harm from occurring even if we ourselves were not responsible (under certain conditions, such as minor self-sacrifice) (Singer, 1972, p. 231). These positions are widely accepted and considered defensible to the minimal degree of having good reasons to act altruistically, regardless of whether they require something of the moral agent. One might therefore accept the onus to aid another at the cost of their own time and effort but would not consider it unjustifiable for another not to do so. If we accept that non-human animals have intrinsic moral worth regardless of their actual or potential relationships with humans, it appears we have good reasons to consider the welfare of wild animals.

Many believe that nature consists of a balance of perpetually stable states, following from which wild animals live happy or contented lives (Zimmerman & Cuddington, 2007, p. 404, Burton, 2015, p. 2).⁷ Because of this, it is assumed that we do not need to be concerned for their individual welfare so long as their natural living conditions are conserved. This attitude is present in welfare science, a seeming candidate for wild animal welfare research. To the extent that welfare science has been concerned with wild animals, this has largely focused on improving their welfare when confined, for example, in zoos (Walker et al. 2014, p. 91). Some efforts have been made to study animal welfare in the wild, but rarely do these extend beyond considering how human activities might impact wild animals either directly (i.e. pest control, harvest management, animal translocation) or indirectly (i.e. deforestation, climate change, natural landscaping).⁸

More commonly, also because of welfare science's historic focus on domestic animal issues, it is accepted that wild animals are sufficiently accounted for by the integrated practices of studies in conservation science. Around the same time of welfare science's emergence in the second half of the twentieth century, ecology and other traditional fields within the life sciences studying natural phenomena gained an ethic of conservation, which developed into the mission-oriented interdisciplinary field of conservation biology (Soule, 1985, p. 727, Meine et al., 2006, p. 636, Franco 2013). Studies in conservation science grew to prominence alongside attitudes of respect for all lifeforms during a period of burgeoning anti-anthropocentric

⁷ The term 'balance' is often used as a metaphor in fields such as population ecology to describe the concept of equilibrium. However, its use has been criticised for being restrictive, value laden, and a general hindrance to understanding relations between natural processes (Sterelny and Griffiths 1999, p. 266, Cuddington 2001).

⁸ Examples include; (Mason and Littin 2003; Littin et al., 2004; Bruce Lauber et al. 2007; Riley et al., 2007; Mafbnz 2010; Harrop 2011; Harrington et al., 2013; Ramp et al., 2016; Dubois et al., 2017).

social dissent (Jamieson, 1998, p. 42).⁹ This gives some context for why, under a paradigm of mutual concern for nonhumans, many believe in the complementary relationship between welfare science and conservation science—the former is seen to address issues affecting the lives of animals living under the domain of humans while the latter deals with issues affecting the lives of animals in the wild.¹⁰

In recent years, however, the underlying consistency of the values represented by these two fields has been challenged by animal ethicists such as Oscar Horta, Catia Faria, Brian Tomasik and others.¹¹ It is argued that the relationship between non-speciesist and conservation-oriented values is misaligned and overstated, highlighted by the emergence of the WWAS concept in which the welfare of animals living in natural ecosystems is overwhelmingly poor. Complementing their work has been research produced and funded by individuals and non-profit organisations under the umbrella of effective altruism, an evidence-based social movement aimed at achieving the most good possible.¹²

Some issues central to the WWAS concept were discussed to some extent by animal ethicists in the years prior. Writers such as Steve Sapontzis, Stephen Clark, Tyler Cowen, Stephen Jay Gould and others brought some of the central philosophical questions of wild animal ethics into focus, such as the moral problem of predation, duties to intervene in nature, and the incommensurability of animal and environmental ethical values.¹³ Precursors to these issues include such philosophers as Arthur Schopenhauer, John Stuart Mill, and Henry Salt, among others.¹⁴ Central figures in the animal ethics orthodoxy have occasionally made comments on issues in wild animal ethics, but rarely do they elaborate on their views in explicit response to the perceived problem of WWAS and all it entails.¹⁵ This we shall now discuss.

⁹ Parallels between these two movements have increased more rapidly in recent years as the environmental impacts of industrial animal agriculture have become more apparent.

¹⁰ Both fields do, of course, overlap in their practice, but it is generally the case that conservation science deals with populations of animals in nature while welfare science deals domestic or human-affiliated animals.

¹¹ Examples include; (Faria 2016b; Horta2010b, 2010c, 2010d, 2013, 2015, 2018; Johannsen 2016, 2017; Keulartz 2016; McMahan 2015; Moen 2016; Palmer 2019; Tomasik 2015; Torres 2015).

 $^{^{12}}$ 'Good' defined by the values held by participants in the movement.

Good defined by the values held by participants in the movement.

¹³ Examples include; (Clark 1979; Cowen 2003; Everett 2001; Fink 2005; Gould 1982; Hadley 2006; McMahan 2010; Næss 1991; Ng 1995; Sapontzis 1984; Simmons 2009).

 ¹⁴ See (Lord Tennyson, 1850, Darwin 1860, Salt 1894, Dunham 2008, p. 119, Mill 2008, Murray 2008, p. 2; Schopenhaur 2010, p. 432).

¹⁵ E.g., Peter Singer's argument from bad consequences (that he later rejects) (Singer, 2015, p. 326, 2016), Tom Regan's appeal to competence (Regan 2004, pp. 357 & 361), Sue Donaldson and Will Kymlicka's 'flourishing' argument applied to sovereign wild animal communities (Donaldson and Kymlicka 2011, pp. 165–167), and Rosalind Hursthouse's appeal to the virtue of respectful love (Hursthouse 2011, p. 133).

The Plight of Wild Animals

The problem of WWAS arises primarily from the interaction between two circumstances that are present in nature; finite resources, and evolutionary processes.¹⁶ Resource scarcity sets a natural limit on resource consumption for a given environment, beyond which the carrying capacity of animals for that environment is exceeded. Such limited resources include energy sources present in one's environment, such as food and water, in addition to structural features that are used for various purposes including shelter and protection. Evolutionary processes are fitnessoriented, meaning that they favour the transmission of heritable traits to optimise gene transmission in the overarching context of an organism's evolution. In response to limiting circumstances such as resource scarcity, evolutionary processes select for traits to improve the fitness of individuals, defined as their ability to survive and reproduce.¹⁷ Typically, these traits are not selected for after an organism has achieved their reproductive potential (depending on their particular life history strategy, this could occur after their first act of successful reproduction or after many such acts).¹⁸

Before we discuss in detail the implications of these combined factors it is worth noting that affective states (manifesting as pleasure, pain, stress, etc., and which constitute at least partially an individual's welfare) are unlikely to have evolved independently from these processes-particularly complex ones which require a significant amount of invested energy to sustain.¹⁹ We can therefore usually assume that the selection of capacities to experience such affective states arose in service of the fitness benefit they provide, and that evolutionary processes are not concerned with welfare beyond the possible utility of such states in motivating behaviour to enhance fitness. Because of this, certain traits that have evolved to increase shortterm survivability might often cause serious harm in the long-term as evidenced by the unfortunate growth pattern of the tusks of the deer pig, or 'babirusa'. By the time certain males have undergone several cycles of reproduction, the curvature of their canines can sometimes grow to puncture their skulls causing a slow and agonising death (Naish, 2010; Panafieu & Gries, 2007). Other cases emerge in elephants whose diets consist of large amounts of dense vegetation which, over time, wears down upon their teeth such that they have evolved to grow back up to six sets over the course of their lifetime. This final set of molars lasts until sometime in their late 50 s, after which these animals face their greatest nonanthropogenic source of mortality; malnutrition and starvation (Pearce, 2015, p. 159).

These are just a few examples to show the diminished relevance of optimised biological states which promote the welfare of individuals following the fulfilment

¹⁶ In addition to other circumstances, such as disease, which we shall discuss later in this section.

¹⁷ 'Survive and reproduce' meaning 'survive to be able to successfully reproduce in accordance with one's evolved life history strategy', as survival does not benefit gene transmission *ipso facto*.

¹⁸ The word 'typically' is used to acknowledge that there is occasionally a substantial inclusive fitness benefit to one's continued survival post-reproduction such that the selection of traits to enhance their survival might still occur, albeit on a lesser basis.

¹⁹ Unless they arise contingently with other selected traits as sometimes happens.

of their fitness potential. But the indifference of natural evolutionary processes to welfare optimisation is not only limited to examples of dysfunctions which might occur after the point at which animals have successfully reproduced and passed on their genes. Bear in mind that under conditions of resource scarcity, adaptions are selected with sole regard to how much they impact fitness, which often results in animals evolving antagonistic and/or predatory relationships with one another. Following this life history strategy many animals have evolved efficient mechanisms to incapacitate and kill individuals from other species, causing them to experience excruciating pain and suffering as a result.

For example; polecats often kill by tossing and rolling around their prey before unleashing a series of bites, redbacked shrikes impale their prey on the thorns of acacia trees for later consumption, and hyena work cooperatively to distract wildebeest and antelope mothers to attack and consume their living offspring (Curio, 1976, pp. 24, 174, 205). A similar tactic is employed by wild dogs whose bites often cause mere immobilisation, allowing the rest of the pack to disembowel and feed upon prey before their actual death. Kelp gulls will sometimes mutilate seal pups by pecking at their eyes with their beaks, electric eels emit a series of short high frequency electric pulses that trigger muscle contraction to immobilize their prey before attacking them, and certain types of piscivorous cone snails use barbed stings to inject fish with paralysing neurotoxins before attempting to swallow them whole (Gallagher et al., 2015, p. 412, Sillar et al., 2016, pp. 156, 330).

Many pain-inducing capacities have also developed in prey species as defensive mechanisms. Certain newt species produce tetrodotoxin—a highly potent poison—to kill snakes that attempt to prey upon them (the same toxin excreted by pufferfish as a means of defence) (McGowan, 1997, p. 59). The Arizona bark scorpion, while also a predator, defends itself from the attacks of desert mice by injecting them once with its barb to "induce an intense burning sensation, followed by several hours of excruciating agony" (Sillar et al., 2016, p. 349). Likewise, while the venom produced by platypus' is not always lethal, there are human reports that it causes "immediate and excruciating pain" which sometimes "develops into a long-lasting hyperalgesia that persists for days or even months" (de Plater et al., 2000, p. 1340). In addition to the defensive ability to produce poisons and venoms, other such capacities as spurs in birds and spikes on porcupines have evolved to help protect prey animals from their predators causing intense suffering (Rand, 1954, p. 131).

Secondary effects of predation might include contributing toward a landscape of fear perceived by animals living in a near-constant state of heightened awareness and stress (Bleicher, 2017; Kohl et al., 2018; Laundré et al., 2001). Findings of PTSD symptoms (memory impairment, learning disability, and other anxiety-related behaviours) in rats exposed to predators indicate that many mammals have the capacity to experience long-lasting psychological distress, which might also extend to other taxonomic groups consisting of animals living in the wild (Zoladz, 2008, pp. 142–143). Other than being unpleasant, feelings of extreme stress which many wild animals experience in response to the perceived threat of predation can even be fatal (Gregory, 2004, p. 18, McCauley et al., 2011, p. 2046). At other times suffering might not be the direct result of predation or resource scarcity. Wild animals are forced to endure extreme weather conditions and natural disaster without relief,

and many suffer from debilitating injuries which drastically reduce their chances of survival.

Disease and parasitism is another significant source of suffering for wildlife, and is typically understated given its prevalence, persistence, and long-term negative effects on the welfare of afflicted hosts (Beldomenico et al., 2008). These include tuberculosis, salmonella, leptospirosis, chlamydia, foot and mouth, herpes, influenza, newcastle, rabies, pox, hantavirus, louping ill, chytridiomycosis, and many parasitic diseases including mange, red mite, cryptosporidiosis, toxoplasmosis, trichromoniasis, lungworm, liver fluke, heartworm, and many others (Boal et al., 1998; Simpson, 2002). Not *all* of these diseases are fatal, however parasitoids necessarily kill their hosts, and often in ways that might involve extreme amounts of suffering. Jewel wasps, for example, administer powerful neurotoxins into the brains of cockroaches making them docile and compliant to predatory mutilation, and will eventually lay an egg for the hatching larva to burrow within its living body and consume its vital organs (Sillar et al. 2016, pp. 343–344).

Disvalue in Reproductive Strategy

In addition to the many difficulties wild animals might expect to face over the course of their lives, it is likely that the main contributor to wild animal suffering comes from the dominant reproductive strategy in nature, which consists in many offspring coming into existence of which only a small percentage survive into adulthood. We have already considered some of the ways in which survival-oriented evolved traits can create excess suffering. But just as the capacity to experience states of welfare did not evolve for the sake of their affective quality per se, traits which prioritise survival are only considered relevant to an animal's fitness to the degree that they help optimise the transmission of their genes.

In humans and other mammals, and in many species of bird, such survival-oriented traits tend to be prioritised in natural selection which constitutes our shared life history strategy of providing parental care and nurturing offspring, eusocial or prosocial behaviour, and flexibility in development to better cope with rapidly shifting environmental conditions. A drawback to this strategy is that it is relatively high risk to invest all of one's energy into one or few offspring whose survival is not guaranteed. Increasing the number of offspring produced by an animal each time they reproduce, or even how often they reproduce, is one way to reduce this risk as there will be more individuals carrying the same set of genes competing against other animals for resources.²⁰ However, by increasing how many offspring are produced per reproduction, the energy that is available to be invested into the development

 $^{^{20}}$ Analysis of trade-offs between these two contrasting reproductive strategies has been termed r/K selection theory (in which r represents a species' maximal intrinsic rate of natural growth, and K represents the carrying capacity of their local environment) (MacArthur and Wilson 1967, Pianka 1970, pp. 292–293). This method of life history classification has since received criticism for oversimplifying the study of population dynamics and producing empirically unsound predictions (Stearns 1992, p. 202, Reznick et al., 2002).

of costly traits to increase survivability is reduced. Over the course of an animal's evolution these values are pushed in the direction of optimisation to account for the limiting conditions of their environment, which constitutes their specific life history strategy.

A good example of this development can be found in the octopus. Octopuses tend to be semelparous, meaning that they evolved to reproduce only once over the course of their lives. This means all of their energy can be directed toward the rearing of a single brood, increasing their reproductive output and the rate at which their offspring become sexually mature (Anderson et al., 2002, p. 281). In fact, certain species of octopus have been observed to lay eggs in the range of hundreds of thousands per clutch (Boyle & Rodhouse, 2005, p. 145). This specific strategy might be beneficial to a population's propagation (promoting gene transmission), but not the welfare of individual members of that population.

To survive for any length of time requires there to be sufficient selection pressure for protection against harmful mutations that cause death and deterioration (Godfrey-Smith, 2016, p. 85). Because octopus larvae hatch in a precocial state of premature self-dependency, there is no significant fitness benefit associated with the continued survival of each parent, which in other circumstances could be needed to protect and rear progeny. Thus, following periods of bountiful reproduction and brooding over clusters of eggs, octopuses enter a state of senescence, dying shortly after their vital functions begin to fail (Anderson et al., 2002, p. 279). In addition, because an organism's natural lifespan is inherently linked to their day-to-day mortality risk, because octopuses occupy the ecological niche of both predator and prey, and because they are so vulnerable to attack having evolved to lose the protective shell of their ammonitic predecessors, octopus life expectancy is considerably diminished beyond the point of their successful reproduction (Godfrey-Smith, 2016, p. 88).

But even if octopuses were to have a longer natural lifespan, their fecundity values guarantee that each time they reproduce, considerably more offspring die shortly after coming into existence than those that can expect to survive into maturity. For a population to remain stable over time, the number of deaths must be matched by the number of individuals who come into existence. How large or small or large these figures are relative to one another is irrelevant so long as they are matched – an animal can produce 10 or even 10,000 offspring over the course of her life with no consequence on the stability of the population so long as only one of those individuals manages to survive to be able to sexually reproduce and continue the cycle of gene transmission.²¹ Animals with higher fecundity values thus have correspondingly higher rates of mortality relative to animals with lower fecundity values (assuming the population is not in a state of growth), and this does not compromise the viability of a population.

²¹ This does not imply that all other offspring members will die prematurely, for many will plausibly survive into their adulthood yet fail to successfully reproduce. Even if all offspring die prematurely a population can remain stable so long as this deficit is compensated for by other reproducing individuals within that same population.

Every animal in nature follows this strategy of reproducing in excess of the carrying capacity of their environment – not just invertebrates such as octopuses. This includes mammals, birds, amphibians, reptiles, and fish, ranging from the low tens to the hundreds of millions of offspring produced (Hapgood, 1979, p. 45, Solbrig & Solbrig, 1979, p. 37, Hinckley, 1987, p. 493, Jeyaseelan, 1998, p. 91). It is, however, important to be clear that although we might choose to identify certain elements of an animal's behaviour with predefined strategies of reproduction, these cannot be used to tell us everything else about their life history. For example, insects tend to have higher rates of fecundity (at extreme variability because of their species richness), which might seem to reduce their likelihood of investing energy into traits that enhance offspring survival at the cost of reproductive potential (Brueland, 1995). But some, like the European earwig, have evolved to provide maternal care for their offspring, while others reproduce in numbers fewer than ten over the course of their lives (Nygård, 1995; Koch & Meunier, 2014, pp. 2–3). While it might be objected that such animals do not suffer as infants, or as invertebrates, inferring sentience in small animals is itself a complex task which we shall address in the next section.

One final point to consider in addition to the copious amounts of suffering wild animals might experience throughout their lives is the possible harm that might be caused by their deaths (as well as the harm of the dying process itself). A common interpretation of the badness of death draws upon a deprivation account whereby there is disvalue if a source of possible value (life) is extinguished – particularly if death occurs prematurely – as this deprives individuals of future goods they might otherwise acquire (Nagel, 1970, p. 74).²² The extent to which the death of wild animals is a deprivation on this account will depend therefore on the possible goods in those animals' lives. It also depends on the degree to which the mental life of animals is unified across the time of their existence such that it is meaningful to say that they have an interest in future goods (DeGrazia, 2016). If they have a life worth living, and some degree of psychological unity, then death is, to that extent at least, bad for them.

We have argued that in many cases it would be an open question whether the life of a wild animal is worth living – plausibly death could be a benign or beneficial deprivation, ending a life of negative welfare. It must be remembered that we are here considering the badness of death itself, independent of the dying process, which will usually cause pain and suffering. Any claim of death liberating an animal from persistent suffering must account for the fact that the dying process will often impose a further welfare cost. And for other animals, death will deprive them of future goods, even under current conditions, while subjecting them to the pain of dying. Given the scale of animal death in the wild, the badness of death adds complexity to the WWAS problem.

²² The simple state of nonexistence is rarely considered an intrinsic source of disvalue, so we shall focus on the deprivation element of being dead.

The Issue of Sentience

One way to reduce the alleged significance of WWAS is to deny that many of the examples of perceived suffering it describes (such as starvation, premature death, and the outcome of antagonistic relations between wild animals) really do constitute harm to animals in all their variety. This position can be supported either by the claim that these purported harmful conditions are in fact benign or beneficial, or by that many animals in those conditions lack the capacity to be harmed. It seems unlikely that all forms of life would have their fitness improved by being able to experience states of affect, which suggests that not all wild animals might have evolved sentience capacities to begin with.²³ Accepting this view has serious consequences for how we conceive the WWAS problem given our current preliminary estimates of how many wild animals are likely to exist at this point in time; wild mammals in the range of 10^{11} to 10^{12} versus for example insects, who number between 10^{17} and 10^{19} (Tomasik, 2018). As we have already argued, the extent to which certain vertebrate groups such as mammals, reptiles, and amphibians (including cephalopods) might already suffer is enormous. If we add the potential suffering of invertebrates such as insects and marine arthropods the scenario becomes factors of times worse with myriads more moral subjects at stake. Issues arise, however, if we attempt to make definitive conclusions regarding whether certain animals are sentient.

First, insects (among other invertebrates) have been the subjects of very little research analysing the state of their cognition and how far their affective capacities might extend (relative to their vertebrate counterparts). And the limited research that does exist often lacks an established methodology, leading to uncertain conclusions when analysing results.²⁴ Something to bear in mind when considering the likelihood of such beings as insects being sentient is that, despite what our intuitions tell us, an absence of evidence does not equate to evidence of an absence. Even until fairly recent years, the claim that all nonhuman animals—even mammals—could experience pain was considered to be unscientific, leading many to assume that in addition to the perceived intractability of studying mental phenomena in nonhumans, these individuals did not have the capacity to experience such conscious states of harm. Thus, we should be wary not to accept preliminary conclusions which result from insufficient data.

Another populous group of animals who do not often have their welfare adequately considered are fishes, who might even exist in numbers higher than 10^{15} . Unlike the current underdeveloped state of sentience research in insects, the topic of fish sentience has been hotly debated in recent years. Neurobiological research on the telencephalon (a subdivision of the fish forebrain) has identified the presence

²³ Barring the acceptance of particular theories of consciousness, such as panpsychism, in which sentience is an intrinsic property of certain natural phenomena rather than an evolved function.

²⁴ Researchers attempting to make progress on this issue include; (Barr et al., 2008; Carder 2017; Diggles 2019; Eisemann et al., 1984; Elwood 2011, 2012; Klein and Barron 2016; Lockwood 1987; Puri and Faulkes 2010; Sømme 2005).

of dopaminergic systems very similar to those responsible for reward conditioning in mammals, corroborated by studies showing their ability to learn to avoid harmful stimuli and then overcome that behaviour under dire conditions (which demonstrates executive function without a neocortex) (Droege & Braithwaite, 2014, p. 91, Sneddon, 2015, p. 970). Further homologies in the nociceptors and nerve fibres possessed by certain fish suggest equivalence in their function, and fish's behavioural response to anaesthetic is consistent with the hypothesis that their mental experience of pain becomes subdued (which is conditional on being able to experience negative mental states to begin with).²⁵

However, sceptics of the fish-pain hypothesis argue that their lack of a forebrain neocortex (and other relevant structures in mammals) render fish incapable of consciously perceiving pain as a negative experience. Rather, fish (and other animals lacking the basic structures they deem necessary for having affective experiences) are said to rely on a more energy-efficient adaptive mechanism for behavioural modification that does not require being conscious of such states.²⁶ The fact that nonhumans lack certain neurobiological features identified as being integral to the experience of pain in humans thus appears to be taken as evidence for their inability to experience such pain states themselves. Mental states are therefore identified *as* physical states of the brain, such that nonhumans, lacking "the right neocortex and the prefrontal neocortex" (as found in the human brain, or one very similar in its structure and composition), do not experience conscious states of pain (Bermond, 2003, p. 83).

The type-identity theory is problematic because it attempts to draw necessary connections between mental states and particular neural structures which may be present or absent in different animals. Accepting that sentience is an evolved trait resulting from the same selective pressures that drive the evolution of other traits within an organism, it is not clear that multiple configurations of neurons, could not perform the same functions in relation to mental states in other animals. The convergent evolution of traits is a well-documented phenomenon across phyla—for example, the wings of bats which are composed of membranous folds of skin tissue, and the eyes of cephalopods which are inverted relative to vertebrate eyes. How these capacities manifest may differ (ie; feathers allow birds to more efficiently glide over long distances, while the elastic and many-jointed structure of bat wings offer a greater degree of manoeuvrability for indoor environments), but they have the same essential function of flight.²⁷

Theories of mind that support the view that mental states can be realised under different conditions (termed 'multiple realizability'), such as in animals from

²⁵ For more discussion, see; (Balcombe 2016; Broom 2016; Browman et al. 2019; Brown 2015; Hurtado-Parrado 2010; Sneddon et al. 2018; Woodruff 2018).

²⁶ For examples, see; (Derbyshire 2016; Hart 2016; Key 2016; Rose 2002, 2007; Rose et al., 2014).

²⁷ Additionally, it is not clear when sentience first emerged in the tree of life. One view, defended in Feinberg and Mallatt's neuroevolutionary account of consciousness, posits that sentience evolved progressively throughout the phylogenetic history of vertebrates, but first appeared very early on during the Cambrian explosion (dating back some 560 or 540–520 mya) (Feinberg and Mallatt 2016, pp. 51 & 117, Godfrey-Smith 2017, p. 63).

different species despite their different neural structures, align better with the evolutionary considerations we present, and support the claim that fish may also suffer, and thus contribute to WWAS.²⁸ While individuals arguing against this possibility are not type-identity theorists per se, the reliance of their arguments upon physical differences between the brains of humans and fish suggest similar theoretical commitments.

A second issue that results from 'drawing the line' on which animals are and are not sentient is that, without having direct access to their minds, such knowledge cannot be obtained with complete certainty. Rather, when we claim that animal 'x' is sentient, we are making an inference based on relevant evidence pertaining to that animal (which might include anatomical similarities, and other forms of evidence). The strength of this inference depends on how convincing we find this evidence, which is liable to change depending on the evidential thresholds and theoretical commitments of different researchers. Importantly, no form of empirical evidence is sufficient to prove the sentience of a given animal, and there are serious risks involved in making such categorical judgements when the stakes involved have normative implications.²⁹

A second response to the alleged significance of WWAS might, rather, attempt to downplay the suffering experienced by infant animals before their premature deaths. Perhaps the plight of these short-living individuals is not relevant to the WWAS problem if their affective capacities are reduced or even non-existent relative to an adult member of their species. It is tempting to think this, being in an underdeveloped state up to the time of their deaths, but this does not conform to our understanding of the adaptive significance of welfare states which exist as tools to motivate behaviour in ways that improve fitness. The absence of parental or community support in their infancy means that many of these animals are born precocial, so adaptive capacities like affective sentience may even be more beneficial for their fitness (applying evolutionary logic). And furthermore, many of these individuals have already been shown to possess a functioning nervous system with pain-suggestive capacities at and before they come into existence, while for others these features develop rapidly with experience of independent life (EFSA 2005, p. 38, Hurtado-Parrado, 2010, p. 665, Lopez-Luna, Al-Jubouri, et al. 2017a, 2017b, 2017c, Lopez-Luna et al., 2017; Lopez-Luna et al., 2017; Lopez-Luna et al., 2017; Lopez-Luna, Canty, et al., 2017).

This is evidence that infant animals across phyla might be sentient, and if sentience is sufficient for ethical importance, then we should care about the suffering that is common in their short lives.

²⁸ A widespread example of such a theory supporting multiple realizability is functionalism, which identifies mental states in terms of the functional roles they play within an organism (Putnam 1975).

²⁹ E.g., even if we assume a 0.01 likelihood that terrestrial arthropods have a mental welfare, and if they do, that their moral standing is only 0.01 compared to a mammal, the case for considering their suffering might be between 10 and 10,000 times that of all extant mammals (Horta, 2010d, p.6) (Soryl, 2020, p.2). These conservative figures are intended to show the risks of ignoring the possible sentience of certain animals belonging to populous taxonomic groups, such as insects and fish.

Canonical Solutions to WWAS

This all shows us that there is a non-negligible possibility that many—perhaps most—animals who are living in the wild experience significant amounts of negative welfare over the course of their lives, plausibly more than positive states of welfare. Insofar as we decide that having a good welfare is something that is intrinsically desirable (desirable for the sake of keeping individuals out of harm's way or allowing them to live meaningful lives for themselves), we ought to be concerned with the welfare of wild animals, and how it can be protected or improved. To this end, we might envision small-scale interventions affecting relatively few individuals with dependable welfare-positive outcomes.³⁰ However, it is difficult to predict the precise effects of large-scale interventions aimed at assisting populations of wild animals, particularly in the long-term, given that our actions might accidentally cause more harm than good if we disrupt the ecosystem in any significant way.

Consider the following case. Leatherback turtles are a group of long-living and highly fecund animals with a unique life history strategy that balances survivability and lifetime reproductive output. Unlike octopuses which are semelparous, leatherback turtles are iteroparous and can reproduce up to nine or ten times over the course of several decades. Since the number of eggs contained within each clutch can exceed 600, adult turtles may produce thousands of offspring over the course of their lifespan, the majority of which are very likely to die before maturing (assuming a stable population size) (Blanvillain et al., 2011, pp. 277–278). If, out of concern for their welfare, we intervene to prevent infant turtles from being preyed upon shortly after their hatching (a significant cause of mortality for members of this species), then more individuals are likely to survive into their adulthood than die prematurely. However, the survival rates of their would-be predators may correspondingly decrease, and other animals sharing their habitat may also experience significant hardship as a result of greater stress on environmental resources, potentially offsetting any good that was otherwise gained by intervening.

Effective action to the end of helping wild animals should seek to treat the root cause of suffering-prevalent ecosystems rather than just their symptoms. All animals naturally reproduce in excess, so while feeding one generation of starving deer might improve their aggregate welfare in the short-term, we cannot expect to achieve the same result indefinitely as future generations come into existence and the demand for food continues to increase ad infinitum.³¹ Avoiding such artificially-induced Malthusian catastrophes when we want to assist wild animals, among other such obstacles, requires that we first introduce welfare as a variable when attempting to model ecological processes such that we can understand its role and function

³⁰ E.g., rescuing and rehabilitating injured and sick wild animals, caring for orphaned infants who are unlikely to survive independently, or assisting animals who are victims of natural disaster. Or even small actions that assist wild animals living in urban environments, such as the regular maintenance and cleaning of bird feeders which both helps starving birds and reduces the transmission of avian disease (Jones and James Reynolds 2008, p. 268, Robb et al. 2008, p. 481).

³¹ Similar circumstances emerge in nature when there are temporarily abundant resources which cause overpopulation termed 'Malthusian checks'.

within natural ecosystems, which itself requires a significant amount of empirical research that does not yet exist.³²

However, by finding out this information we improve our ability to effectively manage the risks involved in providing large-scale relief to wild animals by intervening in nature to protect their welfare. By working to address these issues the problem of WWAS becomes more tractable and we can ensure that our future efforts to assist wild animals are not made in vain, ineffectually, or counterproductively. One way in which this could happen involves the development of a new subfield within welfare science to study the welfare of wild animals—wild animal welfare science, for example—to make progress on the WWAS problem. However, we have reasons to think that this measure alone would not be sufficient.

First, welfare science is a discipline that emerged as a response to concern for the mistreatment of domestic, confined, or in other ways human-affiliated animals, and its conception of welfare developed within these contexts (Broom, 2014). Despite its shared beginnings with the philosophical study of animal ethics, the field has since distanced itself to primarily address *applied* rather than *conceptual* issues in animal mistreatment (Fraser, 1999, p. 173). In doing so, it has been charged for unjustifiably undervaluing animal interests relative to human interests by attempting to help animals within systems which perpetuate morally objectionable human-animal relations.³³ This is relevant to the WWAS problem for reasons of wanting to help improve the welfare of wild animals which results from non-speciesist reasoning held by animal ethicists, as opposed to the unique blend of animal, anthropocentric, and environmental values held in welfare science.

One response to this line of reasoning is that non-speciesist values are not required to study WWAS—we also have epistemic reasons to research this concept in the pursuit of knowledge which have nothing to do with promoting the welfare of individuals. But still, the scope and methodology of welfare science is not entirely suitable to address the WWAS problem. As we have noted earlier, past research in the field primarily consists of welfare assessments on animals used in production systems or contained in zoos. Concern for the welfare of naturally living wild animals tends only to extend insofar as humans are already involved in wildlife interventions for other reasons, such as pest control, resource management, natural landscaping, etc. (Mason & Littin, 2003; Littin et al. 2004; Bruce Lauber et al. 2007, Mafbnz 2010). While welfare science excels at providing a basis for making assessments on animal welfare within such predetermined contexts, there is reason to suspect that the field alone cannot adequately address entire ecosystems containing large numbers of sentient beings with significantly more variables to consider.

Another solution, then, is to select a field that does have a formal history in this area of analysis, such as conservation biology or other fields in the ecological

³² This also involves addressing questions about animal sentience, and possibly even incorporating uncertainty as a variable affecting our conception of welfare, given our earlier discussion about insects and fish.

³³ For examples, see; (Bekoff and Pierce 2016, 2017, p. 25, Donaldson and Kymlicka 2016, Horta 2016, Johannsen 2016, Leadbeater 2016, Marino 2016, Rollin 2019).

sciences with established research methodologies that are attuned to studying entire populations of wild animals. But as we discussed earlier, their accepted value system of conservation appears to handicap the study of welfare for its own sake as an intrinsic good, holding instead that "individual interests and well-being should be subordinated to the holistic good of the earth's biotic community" (Laal, 2009, p. 3). Respect for animals as *individuals* akin to our respect for other humans is shifted to instead respect their rights to live as free agents in nature, emphasising features such as their inclusive fitness and natural history as valid criteria for how we ought to consider their lives (Rolston III 1998, p. 127). For these reasons many consider this position antithetical to the study and perceived significance of WWAS.³⁴

However, recognising these limitations shouldn't lead us to condemn or even reject either of the two fields in their entirety; welfare science has a strong foundation in welfare assessment which is relevant to the suffering of wild animals, while fields within ecology such as conservation biology have expertise in studying wild animal populations. Rather, they show us gaps in current research efforts that could be filled by the creation of an entirely new research field to facilitate research on this topic, perhaps similar in some respects to welfare and conservation science, but different in others so as to recognise WWAS as a problem and further advance the issue of sentience in welfare research. In 1995 Yew Kwang-Ng introduced this prospective discipline termed 'Welfare Biology' and argued in favour of its establishment from the position of evolutionary economics and population dynamics (Ng, 1995). In the years since, despite the interest Ng's work received primarily from philosophers involved in animal ethics, the project of establishing welfare biology has remained largely neglected by scientists who are the ones capable of carrying out its research.

What is Welfare Biology?

A good account of welfare biology describes it as research studying the welfare of all living sentient beings—mostly wild animals, because of the superior numbers—regardless of their living conditions, and independent of their actual or counterfactual relationships with humans or our activities (Ng, 1995). Welfare biology's proposal introduces a potentially more neutral and expansive account of welfare and the value of promoting it compared to welfare science as standardly practised, permitting future research to directly question the legitimacy of orthodoxical paradigms that limit progress on the WWAS problem, like welfare science's focus on animals whose welfare is directly affected by human activities or use of them, such as farming, and conservation science's valuation of natural phenomena as intrinsic goods. The intended outcome of welfare biology research is that we have knowledge of the welfare relations that exist between sentient beings living in nature such that we can make informed judgements about how to improve their welfare if we intend to do so.

³⁴ For many reasons which due to limited space I shall not go into detail about. See; (Sagoff 1984, Mac-Clellan 2012, Paez 2015, Campbell 2018, Faria and Paez 2019) for more discussion on this issue.

A second consideration prompting welfare biology's development is that interest in improving the lives of wild animals already does exist. For decades, actions have been taken to promote wild animal welfare within practices of wildlife management, and there have been many proposals to synthesise the sciences of welfare and conservation.³⁵ But since we haven't yet established a baseline for the quality of life most wild animals experience, any research that attempts to assess the impacts of ethical intervention on behalf of wildlife—say in the practice of wildlife rehabilitation, or humane pest control—operate under the tacit assumption that ecosystems provide acceptable levels of welfare for their constituents.³⁶ As we have established, this should not be assumed to be the case, as it is often not. While these proposals do show a trend in the direction of alignment with non-speciesism, they seem also to emphasise the case for welfare biology's independent development so that we can be more certain that our actions will in fact aid wild animals—considering both the animals that already exist *and* prospective future generations.

Current efforts to promote wild animals within welfare science do not take into account the scale and complexity of ecosystem processes and their bearing on WWAS, so to effectively prescribe action in the field we need to achieve more than mere speculation and surface-level consideration of animals being harmed. Ethological analyses of the possible functions of different states of welfare for different animals contextualised by their distinct evolutionary histories could help us to infer the likelihood individuals belonging to different animal groups being sentient. Theoretical frameworks used in making these inferences should account for the multiple realisability of mental states, complemented by the development of normative frameworks which explicitly account for sentience uncertainty in their derived prescriptions. Lastly, ecological models could tell us how the aggregate welfare of individuals within populations is altered by their activities and by the factors which limit population growth (such as; disease, famine, antagonistic relations between wildlife, etc.), providing us with the necessary data sets to make informed prescriptions to effectively intervene on their behalf.

The current lack of research in these areas relative to other accepted fields in the life sciences involving the use of normative values also gives us a more general picture of how neglected wild animal welfare has been. Welfare biology—despite being proposed more than two decades ago—remains virtually unheard of outside of ethics and philosophy, and it appears that most published research aimed at progressing the issue of WWAS takes place outside of academia and is funded by non-profit research organisations. Compare this to the current state of conservation biology; a well-established mature discipline boasting decades of research toward

³⁵ Compassionate conservation is a good example of this, as well as the more recent proposal of conservation welfare. For examples, see; (Beausoleil et al., 2018; Bekoff 2002; Bekoff and Elzanowski 1997; Bekoff and Jamieson 1996; Fraser 2010; Paquet and Darimont 2010; Ramp and Bekoff 2015; Wallach et al., 2015, 2018).

³⁶ Alternatively, one might acknowledge the problem of WWAS and accept the position that wild animals have a negative welfare yet reject the onus of responsibility placed on humans to aid them. This position has been argued, and (in the authors view) convincingly refuted, in the following texts; (Faria 2015; Palmer 2015).

understanding and solving problems relevant to conservation values. Conservation biology is indeed a good analogue to the prospective discipline given its shared scope, methodology, and incorporation of normative analysis in research that is primarily positive. Furthermore, like conservation biology, welfare biology can be considered a 'crisis discipline', emerging in response to the ongoing issue of WWAS, and requiring the incorporation of various methods and perspectives from other life science fields for it to achieve its objectives.

Conclusion

In this paper we have argued the following: (1) we have good reasons (both moral and epistemic) to conduct further research on the WWAS problem, (2) pre-existing disciplines of animal welfare science and ecology are individually lacking as means for addressing this problem, therefore (3) a synthesis of these fields (termed 'welfare biology') would serve as an effective solution. At present, the prospective discipline of welfare biology has received very little scholarly attention.

At such an early stage in the development of welfare biology it is important to acknowledge the efforts of these organisations aimed at driving growth in the field, but also to emphasise the need for academics—particularly those with expertise in the life sciences—to contribute toward its establishment if it is to become a fully-fledged academic discipline like animal welfare science and conservation biology. It is our hope that this paper motivates readers in this regard. There is much more to be said about the internal dynamics and structure of welfare biology as a new scientific discipline. Since this paper serves as an overview to such issues rather than a detailed exploration of each, we hope for them to be addressed in forthcoming research, either by ourselves or by others working on this important topic.

Acknowledgements We are very grateful for the constructive and insightful comments on an earlier draft of this paper from two anonymous reviewers.

References

- Allen, C., & Bekoff, M. (2007). Animal minds, cognitive ethology, and ethics. *The Journal of Ethics*, 11(3), 299–317.
- Anderson, R. C., Wood, J. B., & Byrne, R. A. (2002). Octopus senescence: The beginning of the end. Journal of Applied Animal Welfare Science, 5(4), 275–283.
- EFSA, E.F.S.A., (2005). Aspects of the Biology and Welfare of Animals Used for Experimental and Other Scientific Purposes, Animal and Welfare Scientific Panel.
- Balcombe, J. (2016). Cognitive evidence of fish sentience. Animal Sentience, 1(3), 2.
- Barr, S., Laming, P. R., Dick, J. T. A., & Elwood, R. W. (2008). Nociception or pain in a decapod crustacean? Animal Behaviour, 75(3), 745–751.
- Beausoleil, N. J., Mellor, D. J., Baker, L., Baker, S. E., Bellio, M., Clarke, A. S., Dale, A., Garlick, S., Jones, B., Harvey, A., Pitcher, B. J., Sherwen, S., Stockin, K. A., & Zito, S. (2018). "Feelings and fitness" not "feelings or fitness"–the raison d'être of conservation welfare, which aligns conservation and animal welfare objectives. *Frontiers in Veterinary Science*, 5(296), 1–14.
- Bekoff, M. (2002). The importance of ethics in conservation biology: Let's be ethicists not ostriches. Endangered Species, 19(2), 23–26.

- Bekoff, M., & Elzanowski, A. (1997). Collecting birds: the importance of moral debate. *Bird Conserva*tion International, 7(4), 357–361.
- Bekoff, M., & Jamieson, D. (1996). Ethics and the study of carnivores: Doing science while respecting animals. In J. L. Gittleman (Ed.), *Carnivore behavior, ecology, and evolution* (pp. 15–45). Cornell University Press.
- Bekoff, M., & Pierce, J. (2016). Animal welfare cannot adequately protect nonhuman animals: The need for a science of animal well-being. *Animal Sentience*, 1(7), 2.
- Bekoff, M., & Pierce, J. (2017). *The animals' agenda: Freedom, compassion, and coexistence in the human age.* Beacon Press.
- Beldomenico, P. M., Telfer, S., Gebert, S., Lukomski, L., Bennett, M., & Begon, M. (2008). Poor condition and infection: A vicious circle in natural populations. *Proceedings of the Royal Society B: Biological Sciences*, 275(1644), 1753–1759.
- Bermond, B. (2003). The myth of animal suffering. In R. G. Botzler & S. J. Armstrong (Eds.), The animal ethics reader (pp. 79–85). Routledge.
- Bleicher, S. S. (2017). The landscape of fear conceptual framework: Definition and review of current applications and misuses. *PeerJ*, 5(9), e3772.
- Blosh, M., (2012). The History of Animal Welfare Law and the Future of Animal Rights. Unpublished thesis. The University of Western Ontario, Ontario.
- Boal, C. W., Mannan, R. W., & Hudelson, K. S. (1998). Trichomoniasis in cooper's hawks from Arizona. Journal of Wildlife Diseases, 34(3), 590–593.
- Boyle, P., & Rodhouse, P. (2005). Cephalopods: Ecology and fisheries. Blackwell Science.
- Broom, D. M. (2011). A history of animal welfare science. ActaBiotheoretica, 59(2), 121-137.
- Broom, D. M. (2014). Sentience and animal welfare. CABI.
- Broom, D. M. (2016). Fish brains and behaviour indicate capacity for feeling pain. Animal Sentience, 1(3), 4.
- Browman, H. I., Cooke, S. J., Cowx, I. G., Derbyshire, S. W. G., Kasumyan, A., Key, B., Rose, J. D., Schwab, A., Skiftesvik, A. B., Stevens, E. D., Watson, C. A., & Arlinghaus, R. (2019). Welfare of aquatic animals: where things are, where they are going, and what it means for research, aquaculture, recreational angling, and commercial fishing. *ICES Journal of Marine Science*, 76(1), 82–92.
- Brown, C. (2015). Fish intelligence, sentience and ethics. Animal Cognition, 18(1), 1–17.
- Bruce Lauber, T., Knuth, B. A., Tantillo, J. A., & Curtis, P. D. (2007). The role of ethical judgments related to wildlife fertility control. *Society & Natural Resources*, 20(2), 119–133.
- Brueland, H., (1995). Highest Lifetime Fecundity. In: University of Florida Book of Insect Records. 41-45.
- Burton, T., (2015). Review of research on public perceptions of naturalness. Nuffield Council on Bioethics.
- Campbell, I. J. (2018). Animal welfare and environmental ethics: It's complicated. *Ethics and the Environment*, 23(1), 49–69.
- Carder, G., (2017). A preliminary investigation into the welfare of lobsters in the UK. Animal Sentience, 2 (16).
- Clark, S. R. L. (1979). The rights of Wild things. Inquiry, 22(1-4), 171-188.
- Cowen, T. (2003). Policing nature. Environmental Ethics, 25(2), 169-182.
- Cuddington, K. (2001). The "balance of nature" metaphor and equilibrium in population ecology. Biology & Philosophy, 16(4), 463–479.
- Curio, E. (1976). The ethology of predation. Springer.
- Darwin, C., (1860). Letter to Asa Gray [online]. Darwin Correspondence Project. Available from: https:// www.darwinproject.ac.uk/letter/DCP-LETT-2814.xml [Accessed 4 Apr 2019].
- Dawkins, M. S. (2017). Animal welfare with and without consciousness. *Journal of Zoology*, 301(1), 1–10.
- de Franco, J. L. A. (2013). The concept of biodiversity and the history of conservation biology: From wilderness preservation to biodiversity conservation. *História (São Paulo)*, 32(2), 21–48.
- de Plater, G. M., Milburn, P. J., & Martin, R. L. (2000). Venom from the platypus, ornithorhynchusanatinus, induces a calcium-dependent current in cultured dorsal root ganglion cells. *Journal of Neurophysiology*, 85(3), 1340–1345.
- Degrazia, D. (1999). Animal ethics around the turn of the twenty-first century. *Journal of Agricultural* and Environmental Ethics, 11(2), 111–129.
- DeGrazia, D. (2016). Sentient nonpersons and the disvalue of death. *Bioethics*, 30(7), 511–519.
- Derbyshire, S. W. G. (2016). Fish lack the brains and the psychology for pain. Animal Sentience, 1(3), 18.

- Diggles, B. K. (2019). Review of some scientific issues related to crustacean welfare. ICES Journal of Marine Science, 76(1), 66–81.
- Donaldson, S. and Kymlicka, W., (2011). Zoopolis: a political theory of animal rights. Oxford; New York: Oxford University Press.
- Donaldson, S., & Kymlicka, W. (2016). Linking animal ethics and animal welfare science. Animal Sentience, 1(5), 5.
- Douglas, H. (2000). Inductive risk and values in science. Philosophy of Science, 67(4), 559-579.
- Droege, P. and Braithwaite, V.A., (2014). A Framework for Investigating Animal Consciousness. In: G. Lee, J. Illes, and F. Ohl, eds. *Ethical Issues in Behavioral Neuroscience*. Berlin, Heidelberg: Springer Berlin Heidelberg, 79–98.
- Dubois, S., Fenwick, N., Ryan, E. A., Baker, L., Baker, S. E., Beausoleil, N. J., Carter, S., Cartwright, B., Costa, F., Draper, C., Griffin, J., Grogan, A., Howald, G., Jones, B., Littin, K. E., Lombard, A. T., Mellor, D. J., Ramp, D., Schuppli, C. A., & Fraser, D. (2017). International consensus principles for ethical wildlife control: Principles for ethical wildlife control. *Conservation Biology*, 31(4), 753–760.
- Dunham, S. A. (2008). The trinity and creation in augustine: An ecological analysis. SUNY Press.
- Eisemann, C. H., Jorgensen, W. K., Merritt, D. J., Rice, M. J., Cribb, B. W., Webb, P. D., & Zalucki, M. P. (1984). Do insects feel pain? — A biological view. *Experientia*, 40(2), 164–167.
- Elwood, R. W. (2011). Pain and suffering in invertebrates? ILAR Journal, 52(2), 175-184.
- Elwood, R. (2012). Evidence for pain in decapod crustaceans. Animal Welfare, 21(1), 23-27.
- Everett, J. (2001). Environmental ethics, animal welfarism, and the problem of predation: A bambi lover's respect for nature. *Ethics & the Environment*, 6(1), 42–67.
- Faria, C., 2015. Disentangling obligations of assistance: A reply to clare palmer's "against the view that we are usually required to assist wild animals". *Relations: Beyond Anthropocentrism*, 3 (2), 211–218.
- Faria, C. (2016a). Animal ethics goes wild: The problem of wild animal suffering and intervention in *nature*. UniversitatPompeuFabra.
- Faria, C., (2016). Why we should not postpone awareness of wild animal suffering, 7 (14), 3
- Faria, C., & Paez, E. (2019). It's splitsville: Why animal ethics and environmental ethics are incompatible. American Behavioral Scientist, 63(8), 1–14.
- Feinberg, T. E., & Mallatt, J. (2016). *The ancient origins of consciousness: How the brain created experience*. The MIT Press.
- Fink, C.K., (2005). The predation argument. Between the Species, 13 (5).
- Fraser, D. (1999). Animal ethics and animal welfare science: Bridging the two cultures. *Applied Animal Behaviour Science*, 65(3), 171–189.
- Fraser, D., (2008). Understanding animal welfare: the science in its cultural context. Oxford; Ames, Iowa: Wiley-Blackwell.
- Fraser, D. (2010). Toward a synthesis of conservation and animal welfare science. *Animal Welfare*, 2(19), 121–124.
- Gallagher, A., Staaterman, E., & Dreyer, N. (2015). Kelp gulls prey on the eyes of juvenile Cape fur seals in Namibia. African Journal of Marine Science, 37(3), 411–414.
- Godfrey-Smith, P. (2016). Other minds: the octopus, the sea, and the deep origins of consciousness. Farrar, Straus and Giroux.
- Godfrey-Smith, P. (2017). Animal evolution and the origins of experience. In D. L. Smith (Ed.), *How biology shapes philosophy* (pp. 51–71). Cambridge University Press.
- Gould, S. J. (1982). Nonmoral nature. Natural History, 91, 19-26.
- Gregory, N. G. (2004). Physiology and behaviour of animal suffering. Blackwell.
- Hadley, J. (2006). The duty to aid nonhuman animals in dire need. *Journal of Applied Philosophy*, 23(4), 445–451.
- Hapgood, F. (1979). Why males exist, an inquiry into the evolution of sex. Morrow.
- Harrington, L. A., Moehrenschlager, A., Gelling, M., Atkinson, R. P. D., Hughes, J., & Macdonald, D. W. (2013). Conflicting and complementary ethics of animal welfare considerations in reintroductions: Welfare in reintroductions. *Conservation Biology*, 27(3), 486–500.
- Harrop, S. (2011). Climate change, conservation and the place for wild animal welfare in international law. *Journal of Environmental Law*, 23(3), 441–462.
- Hart, P. J. B. (2016). Fighting forms of expression. Animal Sentience, 1(3), 9.
- Hinckley, S. (1987). The reproductive biology of walleye pollock, theragrachalcogramma, in the bering sea, with reference to spawing stock. *Structure*, 85(3), 481–498.

- Horta, O. (2010a). What is speciesism? Journal of Agricultural and Environmental Ethics, 23(3), 243–266.
- Horta, O. (2010b). Debunking the idyllic view of natural processes: Population dynamics and suffering in the wild. *Revistalberoamericana de EstudiosUtilitaristas*, 17(1), 73–90.
- Horta, O. (2010c). The ethics of the ecology of fear against the nonspeciesist paradigm: A shift in the aims of intervention in nature. *Between the Species: An Online Journal for the Study of Philosophy* and Animals, 13(10), 163–187.
- Horta, O., (2010). Disvalue in nature and intervention. Pensata Animal, 34.
- Horta, O. (2013). Zoopolis, Intervention, and the State of Nature. Law, Ethics, and Philosophy, 1, 113–125.
- Horta, O., (2015). The problem of evil in nature: Evolutionary bases of the prevalence of disvalue. *Relations: Beyond Anthropocentrism*, 3 (2), 17–32.
- Horta, O. (2016). Changing attitudes towards animals in the wild and speciesism. *Animal Sentience*, *3*(7), 15.
- Horta, O. (2018). Concern for wild animal suffering and environmental ethics: What are the limits of the disagreement? Les ateliers de l'éthique, 13(1), 85.
- Hursthouse, R., (2011). Virtue Ethics and the Treatment of Animals. In: T.L. Beauchamp and R.G. Frey, eds. The Oxford Handbook of Animal Ethics. Oxford University Press, 119–143.
- Hurtado-Parrado, C. (2010). Neuronal mechanisms of learning in teleost fish. UniversitasPsychologica, 9(3), 663–678.
- Jamieson, D. (1998). Animal liberation is an environmental ethic. Environmental Values, 7(1), 41-57.
- Jamieson, D., & Bekoff, M. (1990). Cognitive ethology and applied philosophy: The significance of an evolutionary biology of mind. *Trends in Ecology & Evolution*, 5(5), 156–159.
- Jeyaseelan, M. J. P. (1998). *Manual of fish eggs and larvae from Asian mangrove waters*. United Nations Educational.
- Johannsen, K. (2016). Animal welfare at home and in the wild. Animal Sentience, 1(7), 10.
- Johannsen, K. (2017). Animal rights and the problem of r-strategists. *Ethical Theory and Moral Practice*, 20(2), 333–345.
- Jones, D. N., & James Reynolds, S. (2008). Feeding birds in our towns and cities: A global research opportunity. *Journal of Avian Biology*, 39(3), 265–271.
- Keulartz, J. (2016). Should the lion eat straw like the Ox? Animal ethics and the predation problem. Journal of Agricultural and Environmental Ethics, 29(5), 813–834.
- Key, B., 2016. Why fish do not feel pain. Animal Sentience, 1 (3).
- Klein, C. and Barron, A.B., (2016). Insects have the capacity for subjective experience. *Animal Sentience*, 1 (9).
- Koch, L. K., & Meunier, J. (2014). Mother and offspring fitness in an insect with maternal care: Phenotypic trade-offs between egg number, egg mass and egg care. *BMC Evolutionary Biology*, 14(1), 1–9.
- Kohl, M. T., Stahler, D. R., Metz, M. C., Forester, J. D., Kauffman, M. J., Varley, N., White, P. J., Smith, D. W., & MacNulty, D. R. (2018). Diel predator activity drives a dynamic landscape of fear. *Ecological Monographs*, 88(4), 638–652.
- Laal, M. (2009). A brief history of enviroethics and its challenges. *Journal of Medical Ethics and History of Medicine*, 2(10), 5.
- Laundré, J.W., Hernández, L., and Altendorf, K.B., (2001). Wolves, elk, and bison: reestablishing the 'landscape of fear' in Yellowstone National Park, U.S.A. *Canadian Journal of Zoology*, 79 (8), 1401–1409.
- Leadbeater, S. (2016). Animal suffering calls for more than a bigger cage. Animal Sentience, 1(7), 4.
- Littin, K., Mellor, D., Warburton, B., & Eason, C. (2004). Animal welfare and ethical issues relevant to the humane control of vertebrate pests. *New Zealand Veterinary Journal*, 52(1), 1–10.
- Lockwood, J. A. (1987). The moral standing of insects and the ethics of extinction. *The Florida Ento*mologist, 70(1), 70–89.
- Lopez-Luna, J., Al-Jubouri, Q., Al-Nuaimy, W., & Sneddon, L. U. (2017). Impact of analgesic drugs on the behavioural responses of larval zebrafish to potentially noxious temperatures. *Applied Animal Behaviour Science*, 188, 97–105.
- Lopez-Luna, J., Al-Jubouri, Q., Al-Nuaimy, W., & Sneddon, L. U. (2017). Reduction in activity by noxious chemical stimulation is ameliorated by immersion in analgesic drugs in zebrafish. *Journal of Experimental Biology*, 220(8), 1451–1458.

- Lopez-Luna, J., Al-Jubouri, Q., Al-Nuaimy, W., & Sneddon, L. U. (2017). Impact of stress, fear and anxiety on the nociceptive responses of larval zebrafish. *PLoS ONE*, 12(8), e0181010.
- Lopez-Luna, J., Canty, M. N., Al-Jubouri, Q., Al-Nuaimy, W., & Sneddon, L. U. (2017). Behavioural responses of fish larvae modulated by analgesic drugs after a stress exposure. *Applied Animal Behaviour Science*, 195, 115–120.
- Lord Tennyson, A., (1850) In Memoriam A. H. H. OBIIT MDCCCXXXIII: 55 [online]. Poetry Foundation. Available from: https://www.poetryfoundation.org/poems/45342/in-memoriam-a-h-h-obiitmdcccxxxiii-55 [Accessed 14 May 2019].
- Lund, V., Mejdell, C., Röcklinsberg, H., Anthony, R., & Håstein, T. (2007). Expanding the moral circle: Farmed fish as objects of moral concern. *Diseases of Aquatic Organisms*, *75*, 109–118.
- MacArthur, R. H., & Wilson, E. O. (1967). *The theory of island biogeography*. Princeton University Press.
- MacClellan, J.P., (2012). Minding Nature: A Defense of a Sentiocentric Approach to Environmental Ethics. Unpublished thesis. University of Tennessee.
- MAFBNZ, (2010). *How humane are our pest control tools?* Lincoln: MAFBNZ Operational Research, MAF Biosecurity New Zealand Technical Paper No: 2011/01 No. 09–11326.
- Marino, L. (2016). Why animal welfarism continues to fail. Animal Sentience, 1(7), 5.
- Mason, G., & Littin, K. E. (2003). The humaneness of rodent pest control. Animal Welfare, 12, 1-37.
- McCauley, S. J., Rowe, L., & Fortin, M. J. (2011). The deadly effects of "nonlethal" predators. *Ecology*, 92(11), 2043–2048.
- McGowan, C. (1997). The raptor and the lamb: Predators and prey in the living world. Henry Holt and Company.
- McMahan, J., 2010. The Meat Eaters [online]. New York Times, Sep 19. Available from: https://opinionator.blogs.nytimes.com/2010/09/19/the-meat-eaters/ [Accessed 23 Sep 2019].
- McMahan, J. (2015). The Moral Problem of Predation. In A. Chignell, T. Cuneo, & M. C. Halteman (Eds.), *Philosophy comes to dinner: Arguments about the ethics of eating* (pp. 268–294). Routledge.
- Meine, C., Soule, M., & Noss, R. F. (2006). 'A mission-driven discipline': The growth of conservation biology. *Conservation Biology*, 20(3), 631–651.
- Mellor, D. J., Patterson-Kane, E., & Stafford, K. J. (2009). The Sciences of animal welfare. Wiley-Blackwell.
- Mill, J.S., 2008. On Nature [online]. Early Modern Texts. Available from: https://www.earlymoderntexts. com/assets/pdfs/mill1873b.pdf [Accessed 23 Sep 2019].
- Moen, O. M. (2016). The ethics of wild animal suffering. *Etikkipraksis Nordic Journal of Applied Ethics*, 10(1), 91–104.
- Murray, M.J., (2008). *Nature red in tooth and claw: Theism and the problem of animal suffering*. Oxford; New York: Oxford University Press.
- Næss, A. (1991). Should we try to relieve clear cases of suffering in nature? Pan Ecology, 6(1), 1-5.
- Nagel, T. (1970). Death. Noûs, 4(1), 73-80.
- Naish, D., 2010. Babirusas can get impaled by their own teeth: that most sought-after of objects does exist! [online]. *ScienceBlogs*. Available from: https://scienceblogs.com/tetrapodzoology/2010/03/ 08/babirusa-impales-own-head [Accessed 15 Aug 2019].
- Ng, Y.-K. (1995). Towards welfare biology: Evolutionary economics of animal consciousness and suffering. *Biology & Philosophy*, 10(3), 255–285.
- Nussbaum, M.C., (2006). Frontiers of justice: disability, nationality, species membership. Cambridge, Mass: The Belknap Press: Harvard University Press.
- Nygård, B.C., (1995). Lowest lifetime fecundity. In: University of Florida Book of Insect Records. 39-40.
- Paez, E., (2015). Refusing help and inflicting harm: A critique of the environmentalist view. *Relations: Beyond anthropocentrism*, 3 (2), 165–178.
- Palmer, C., (2015). Against the view that we are normally required to assist wild animals. *Relations: Beyond Anthropocentrism*, 3(2), 203–210.
- Palmer, C. (2019). Assisting wild animals vulnerable to climate change: Why ethical strategies diverge. Journal of Applied Philosophy, online first publication. https://doi.org/10.1111/japp.12358
- Panafieu, J.-B., & Gries, P. (2007). Evolution. Seven Stories Press.
- Paquet, P. C., & Darimont, C. T. (2010). Wildlife conservation and animal welfare: Two sides of the same coin? *Animal Welfare*, 19, 177–190.
- Pearce, D., (2015). A welfare state for elephants? A case study of compassionate stewardship. *Relations: Beyond anthropocentrism*, 3(2), 153–164.

Pianka, E. R. (1970). On r- and K-selection. The American Naturalist, 104(940), 592-597.

- Puri, S., & Faulkes, Z. (2010). Do decapod crustaceans have nociceptors for extreme pH? *PLoS ONE*, 5(4), e10244.
- Putnam, H. (1975). The nature of mental states. *Philosophical papers: Mind, language, and reality* (pp. 429–440). Cambridge University Press.
- Ramp, D., & Bekoff, M. (2015). Compassion as a practical and evolved ethic for conservation. *BioScience*, 65(3), 323–327.
- Ramp, D., Wilson, V., & Croft, D. (2016). Contradiction and complacency shape attitudes towards the toll of roads on wildlife. *Animals*, 6(40), 1–15.
- Rand, A. L. (1954). On the spurs of birds' wings. The Wilson Bulletin, 66(2), 127-134.
- Regan, T. (2004). The case for animal rights. Updated (2004th ed.). California.
- Reznick, D., Bryant, M. J., & Bashey, F. (2002). r- and K-selection revisited: The role of population regulation in life-history evolution. *Ecology*, 83(6), 1509–1520.
- Riley, S. P. D., Bromley, C., Poppenga, R. H., Uzal, F. A., Whited, L., & Sauvajot, R. M. (2007). Anticoagulant exposure and notoedric mange in bobcats and mountain lions in Urban Southern California. *Journal of Wildlife Management*, 71(6), 1874–1884.
- Robb, G. N., McDonald, R. A., Chamberlain, D. E., & Bearhop, S. (2008). Food for thought: Supplementary feeding as a driver of ecological change in avian populations. *Frontiers in Ecology and the Environment*, 6(9), 476–484.
- Rollin, B. E. (2019). Progress and absurdity in animal ethics. *Journal of Agricultural and Environmental Ethics*, 32, 391–400.
- Rolston, H., III. (1998). Challenges in environmental ethics. In M. E. Zimmerman, J. B. Callicott, G. Sessions, K. J. Warren, & J. Clark (Eds.), *Environmental philosophy: From animal rights to radical ecology* (pp. 124–144). Prentice Hall.
- Rose, J. D. (2002). The neurobehavioral nature of fishes and the question of awareness and Pain. *Reviews* in Fisheries Science, 10(1), 1–38.
- Rose, J. (2007). Anthropomorphism and 'mental welfare' of fishes. *Diseases of Aquatic Organisms*, 75, 139–154.
- Rose, J. D., Arlinghaus, R., Cooke, S. J., Diggles, B. K., Sawynok, W., Stevens, E. D., & Wynne, C. D. L. (2014). Can fish really feel pain? *Fish and Fisheries*, 15(1), 97–133.
- Sagoff, M. (1984). Animal liberation and environmental ethics: bad marriage quick divorce. Osgoode Hall Law Journal, 22(2), 297–307.
- Salt, H. S. (1894). Animals' rights: Considered in relation to social progress. Macmillan & Co.
- Sapontzis, S. F. (1984). Predation. Ethics and Animals, 5(2), 27-38.
- Schopenhaur, A. (2010). On the sufferings of the world. In D. Benatar (Ed.), Life, death, and meaning: Key philosophical readings on the big questions (pp. 431–440). Rowman & Littlefield Publishers.
- Sillar, K. T., Picton, L. D., & Heitler, W. J. (2016). *The neuroethology of predation and escape*. West Sussex: Wiley.
- Simmons, A. (2009). Animals, predators, the right to life, and the duty to save lives. *Ethics & the Environment*, 14(1), 15–27.
- Simpson, V. R. (2002). Wild animals as reservoirs of infectious diseases in the UK. The Veterinary Journal, 163(2), 128–146.
- Singer, P. (1972). Famine, affluence, and morality. Philosophy and Public Affairs, 1(3), 229-243.
- Singer, P., (2015). *Animal Liberation: The Definitive Classic of the Animal Movement*. 40th Anniversary Edition. Open Road Media.
- Singer, P., (2016). The Suffering of Wild Animals: Should we do anything about it, and if so, what? [online]. *High Meadows Environmental Institute*. Available from: https://www.youtube.com/ watch?v=1VYYHLH990A [Accessed 4 Apr 2019].
- Sneddon, L. U. (2015). Pain in aquatic animals. Journal of Experimental Biology, 218(7), 967–976.
- Sneddon, L.U., Lopez-Luna, J., Wolfenden, D.C.C., Leach, M.C., Valentim, A.M., Steenbergen, P.J., Bardine, N., Currie, A.D., Broom, D.M., and Brown, C., (2018). Fish sentience denial: Muddying the waters. *Animal Sentience*, 21 (1).
- Solbrig, O. T., & Solbrig, D. J. (1979). Introduction to population biology & evolution. Addison-Wesley.
- Sømme, L.S., (2005). Sentience and Pain in Invertebrates. Dept. of Animal and Aquacultural Sciences: Norwegian University of Life Sciences, Report to Norwegian Scientific Committee for Food Safety.
- Soule, M. E. (1985). What is conservation biology? BioScience, 35(11), 727-734.

Stearns, S. C. (1992). The evolution of life histories. Oxford University Press.

- Sterelny, K., & Griffiths, P. (1999). Sex and death: An introduction to philosophy of biology. University of Chicago Press.
- Tomasik B (2015) The Importance of Wild-Animal Suffering. *Relations: Beyond Anthropocentrism*, 3(2), 133–152.
- Tomasik, B., 2018. How Many Wild Animals Are There? [online]. *Reducing Suffering*. Available from: https://reducing-suffering.org/how-many-wild-animals-are-there/ [Accessed 31 Jan 2019].
- Torres, M., (2015) The Case for Intervention in Nature on Behalf of Animals: A Critical Review of the Main Arguments against Intervention. *Relations: Beyond Anthropocentrism*, 3 (2), 33–49.
- Vauclair, J. (1997). Mental states in animals: Cognitive ethology. *Trends in Cognitive Sciences*, 1(1), 35–39.
- Walker, M., Díez-León, M., & Mason, G. (2014). Animal Welfare Science: Recent publication trends and future research priorities. *International Journal of Comparative Psychology*, 27(1), 80–100.
- Wallach, A. D., Bekoff, M., Batavia, C., Nelson, M. P., & Ramp, D. (2018). Summoning compassion to address the challenges of conservation: Compassionate conservation. *Conservation Biology*, 32(6), 1255–1265.
- Wallach, A. D., Bekoff, M., Nelson, M. P., & Ramp, D. (2015). Promoting predators and compassionate conservation: Predators and compassionate conservation. *Conservation Biology*, 29(5), 1481–1484.
- Woodruff, M. L. (2018). Pain in fish: Evidence from peripheral nociceptors to pallial processing. Animal Sentience, 3(21), 2.
- Zimmerman, C., & Cuddington, K. (2007). Ambiguous, circular and polysemous: Students' definitions of the "balance of nature" metaphor. *Public Understanding of Science*, 16(4), 393–406.
- Zoladz, P.R., (2008). An ethologically relevant animal model of post-traumatic stress disorder: Physiological, pharmacological and behavioral sequelae in rats exposed to predator stress and social instability. Unpublished thesis. University of South Florida.

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.