Check for
updates

Does suffering dominate enjoyment in the animal kingdom? An update to welfare biology

Zach Groff[1] [ORCID] · **Yew-Kwang Ng**[2]

Abstract

Ng (Biol Philos 10(3):255–285, 1995. https://doi.org/10.1007/bf00852469) models the evolutionary dynamics underlying the existence of suffering and enjoyment and concludes that there is likely to be more suffering than enjoyment in nature. In this paper, we find an error in Ng's model that, when fixed, negates the original conclusion. Instead, the model offers only ambiguity as to whether suffering or enjoyment predominates in nature. We illustrate the dynamics around suffering and enjoyment with the most plausible parameters. In our illustration, we find surprising results: the rate of failure to reproduce can improve or worsen average welfare depending on other characteristics of a species. Our illustration suggests that for organisms with more intense conscious experiences, the balance of enjoyment and suffering may lean more toward suffering. We offer some suggestions for empirical study of wild animal welfare. We conclude by noting that recent writings on wild animal welfare should be revised based on this correction to have a somewhat less pessimistic view of nature.

Keywords Animal welfare · Animal suffering · Welfare biology · Effective altruism · Evolutionary biology

Introduction

In 1995, following the idea that scientists and economists should treat animal welfare as important in its own right, Ng proposed the study of welfare biology, with three basic questions: Which animals are capable of welfare? Is their welfare

✉ Zach Groff
zgroff@stanford.edu

Yew-Kwang Ng
kwang.ng@monash.edu

[1] Department of Economics, Stanford University, Stanford, CA, USA

[2] School of Economics, Fudan University, Shanghai, China

positive or negative? How can we increase their welfare? In particular, Ng argued that science should examine not only the welfare of animals currently used by humans but also, and perhaps more importantly, the wellbeing of animals living in the wild. Ng's argument relates to the predation problem in moral philosophy, or the issue of whether animal rights requires humans to save prey from predators. Originally proposed as a reduction ad absurdum of animal rights, the predation problem has prompted a number of responses from moral philosophers ranging from principles of non-intervention to denials of feasibility to acceptance of an obligation to help only in dire cases (Clark 1979). Still others do not find available responses to the predation problem convincing, which motivates Ebert and Machan (2012) to promote a "libertarian-ish theory of animal rights." On any view that is not strictly non-interventionist, an understanding of wild-animal wellbeing is useful. Furthermore, such an understanding is interesting in itself and may yield insights relevant to other problems, so Ng (1995) investigates the balance of suffering and enjoyment in nature.

The question of natural suffering extends beyond the predation problem to disease, starvation, and daily stress. In recent years, a number of prominent thinkers in and beyond economics have weighed in on the possibility of stewarding nature to promote animal wellbeing. Economist, political theorist, and popular blogger Tyler Cowen argues for "modest steps to limit or check the predatory activity of carnivores relative to their victims," including not protecting or reintroducing predators in natural areas (2003). Oxford philosopher Jeff McMahan argues—in *The New York Times*, no less—that people of good will should hope for the gradual extinction of predatory species (2010). Even Matthews of the popular news site *Vox* asks philosopher Peter Singer in a 2015 interview whether humans should intervene in nature and what questions those researching wild animal welfare should be asking (Matthews 2015).

Several organizations now work on and research wild-animal welfare, including the Wild Animal Welfare Committee, Wild Animal Initiative, and Animal Ethics. The first of these groups aims to apply the ideal of "guardianship" developed by the Farm Animal Welfare Committee to conservation and environmental management programs that, to date, have largely focused on species' continuation rather than individual animals' welfare (Wild Animal Welfare Committee 2019). The latter two groups are associated with what is known as the "effective altruism" movement, a group of philanthropists, advocates, and researchers who in their words aim to do good as effectively as possible. Many in the effective altruism movement believe that animals' interests should matter equally to those of humans and see little difference between actively hurting someone and failing to help someone in need, all else equal. For these reasons, it is a natural concern for the effective altruism movement that there may be a large number of wild animals suffering in ways that may be able to be at least partially alleviated. All three organizations are fairly young, suggesting that interest in the topic is growing among nonprofits.

Outside of philanthropy, academic biologists and environmental policymakers also deal regularly with questions explicitly or implicitly tied to wild-animal welfare on a routine basis. Though environmental policies are more commonly designed to preserve species rather than to protect animals, compassion for animals often

does motivate policies, and so policies' effects on individual animals are well worth considering.

Research into what Ng (1995) terms "welfare biology" is therefore a high-priority, highly neglected field. To date, virtually all research into human impacts on nature focuses narrowly on the conservation of species and ecosystem dynamics. Most theories in environmental ethics assign instrumental or even intrinsic value to natural processes, but few locate value within individual wild animals. Ng's paper proposed a new angle to study animals in nature and humans' effects on them.

Ng (1995) discusses a number of critical topics in welfare biology. Ng addresses questions of which animals experience emotional states, which states they experience, and how humans can improve wild animal wellbeing. Ng notes that suffering and enjoyment likely serve evolutionary purposes.

In this paper, we make a correction to Ng's (1995) proposition that total suffering in nature outweighs total enjoyment. In fact, as we show, total enjoyment may exceed total suffering or vice versa, depending on a specific evolutionary detail for which we have little information. We propose a revised version of the Buddhist Premise that suffering predominates in nature. Under the revised proposition, there is little reason to conclude one way or another whether suffering or enjoyment is more common. After presenting the revised Buddhist premise, we note an interesting tradeoff between the number of animals who suffer and the degree of those animals' suffering. We illustrate these dynamics based on plausible assumptions from psychology. Finally, we offer some guidance for how other researchers in this area can make progress and how recent research should be updated based on this revision of the Buddhist premise.

The revised Buddhist premise

An important question regarding animal welfare is whether, on average, animals enjoy positive net welfare. This is the second of three basic questions Ng (1995) raises; the other two questions are the 'which' question (which organisms are capable of welfare) and the 'how' question (how to increase their welfare).

This first question is crucial. For example, if the answer is that animals on the whole enjoy negative (net) welfare, many people may find it more imperative for us humans to try to increase their welfare to a non-negative level. In some extreme cases, some authors regard animal suffering (negative net welfare) as justifying the destruction of animal habitats (Tomasik 2016). Ng hopes for future improvement of animals' welfare after significant scientific, economic, and ethical advances on the part of humans (Ng 1995, 2016b).

Ng (1995) argues that animals suffer from negative net welfare on the whole. Ng uses both a general argument and an 'economics of evolution'. The general argument is based on the observation that most animal species have large clutch sizes and a presumption (related to the economics of evolution) that individual animals not able to survive until mating probably suffer from negative net welfare.

The economics of evolution led Ng to propose the following:

Proposition (Buddhist Premise) *Under the assumptions of concave and symmetrical functions relating costs to enjoyment and suffering, evolutionary economizing results in the excess of total suffering over total enjoyment.*

This premise, it turns out, does not hold. Ng's conditions have to be strengthened to make the proposition valid. The revised Buddhist premise we wish to propose is remarkable and has the same remarkable implications should the updated conditions hold, but whether the new conditions hold is a matter of further research and does not evoke any obvious intuition.

Instead, we propose the following, corrected version of the Buddhist Premise:

Revised Proposition (Buddhist Premise) *Under the assumption of symmetrical functions relating costs to enjoyment and suffering, evolutionary economizing results in the excess of total suffering over total enjoyment if the square of each function is concave.*

We sketch the reasoning behind this revised proposition here as well as the error in the original intuition. The 'proof' of the Buddhist proposition was provided in "Appendix" section in Ng (1995). Let E represent the amount of enjoyment experienced by organisms who successfully reproduce and S the amount of suffering experienced by organisms that fail to reproduce, and let n > 1 be the number of failing organisms relative to the number of successful ones. Finally, let C_E and C_S be the evolutionary cost of producing that enjoyment and suffering, respectively. Let $E(C_E)$ and $S(C_S)$ be concave functions, as should be expected (Ng 1995). Ng (1995) shows, based on an evolutionary constrained optimization, that $nE'(C_E) = S'(C_S)$. Ng (1995) then argues using a geometric figure that the total amount of suffering exceeds the total amount of enjoyment, that is $nS > E$.

The geometric intuition does not actually hold, though. For instance, if $E(C_E) = C_E^{\frac{3}{4}}$, and $E(C_S) = C_S^{\frac{1}{4}}$, then in equilibrium $E = n^3 S$, which of course is greater than nS. More generally, for any function of the form $E(C_E) = (C_E)^\alpha$ with $\alpha > 1/2$ (and $S(C_S)$ similarly defined), there is in fact an excess of total enjoyment over total suffering, even though the function is concave.

We can see the correct conditions for the Buddhist Premise by the following logic. Ng (1995) proves that in equilibrium the following holds for smooth functions:

$$nE'(C_E) = S'(C_S) \tag{1}$$

This can be easily rearranged to give:

$$n = \frac{S'(C_S)}{E'(C_E)} \tag{2}$$

We want a condition for the functions $E(C_E)$ and $S(C_S)$ that implies that $nS > E$. Plugging in the value of n for Eq. (2), we want to know for which smooth, symmetrical, increasing, concave functions $E(C_E)$ and $S(C_S)$ the following holds:

$$S(C_S)S'(C_S) > E(C_E)E'(C_E) \tag{3}$$

This inequality is equivalent to the following:

$$S^{2\prime}(C_S) > E^{2\prime}(C_E) \tag{4}$$

That is, we want a function for $E(C_E)$ and $S(C_S)$ such that the derivative of the square of the function is greater for $S(C_S)$ than for $E(C_E)$. Since $C_S < C_E$, this follows from concavity of the function squared. Therefore, total suffering will exceed total enjoyment if the square of the function is concave.[1]

In its earlier, incorrect form, the premise relied on conditions that one would reasonably expect to hold. As Ng (1995) lays out, there is no reason to expect suffering or enjoyment to be inherently easier to produce, so the functions should be symmetrical. There is no obvious, pre-existing body of research on evolutionary cost functions for suffering and enjoyment, but the few parallels that do exist suggest that the functions should be concave. An established finding in psychology is that animals and humans habituate over time to repeated stimuli (Thompson and Spencer 1966; Rankin et al. 2009). In economics, while the use of cardinal utility functions is controversial, those who examine cardinal utility functions hold that utility should generally exhibit diminishing marginal returns (Gossen 1854/1983; Harsanyi 1953, 1955).[2] A recent paper combining experimental evidence with a meta-analysis finds that, in fact, humans and animals share similar behavior with regard to risk, and this behavior relates to diminishing responses to stimuli (Weber et al. 2004). Taken together, this research indicates that to the extent we can compare utility across animals and humans, both negative and positive utility should be concave. On this basis, the original Buddhist Premise offered a remarkable conclusion.

The revised proposition leads to a different conclusion: at least based on evolutionary theory alone, we should be agnostic with regard to whether total suffering will exceed enjoyment or vice versa. There is no obvious evidence in biological literature as to whether the square of the production functions for affective experiences should be concave. The question of how evolution produces suffering and enjoyment is highly uncertain; in pondering the question, we can only find parallels rather than direct evidence. The available parallels narrowly suggest the function is more likely to be concave than not, but they give rise to no clear intuition about the square of the function.

The intuition behind the original Buddhist Premise miscalculates a subtle tradeoff in the evolutionary production of animals' experiences. As the number of organisms in a

---

[1] It may be the case, of course, that the concavity of the square of a function changes over its domain, so while this condition is sufficient, it is not necessary.

[2] Evidence of concave utility functions in economics traditionally draws on research into risk aversion, which shows that averaging a concave (Bernoulli) utility function across possible outcomes gives rise to risk-averse behavior (Pratt 1964). Behavioral economics modifies the traditional picture of risk aversion to include the possibility of loss aversion, where both the utility of gains and negative utility of losses are concave (Tversky and Kahneman 1992).

While Tversky and Kahneman's finding supports the concavity of suffering and enjoyment, it may seem to undermine the claim of symmetry because people tend to weigh losses more than gains. On further inspection, this result is entirely consistent with symmetric evolutionary cost functions based on the simple fact that apparent losses in the wild more often pose a risk of failure to survive than successes. Weber et al. (2004) note that prospect theory closely represents the energy budget rule for animals' risk-related behavior (Caraco 1980; Stephens 1981), because apparent losses generally pose a greater risk of starvation than equally-sized apparent gains. This implies that even if the evolutionary costs of suffering and enjoyment are identical, organisms should be more averse to losses than to gains. Hence available evidence is consistent with symmetrical functions for the evolutionary cost of suffering and enjoyment.

species who fail to reproduce increases, two shifts happen, one of which drives the net balance of suffering up, and the other which drives the net balance of suffering down. First and most obviously, the more organisms in a species fail, the more cases of suffering there are relative to enjoyment. That is, in studying the inequality $nS > E$, the value of n goes up. This is the intuition that motivates Ng and others to conclude that nature is likely dominated by suffering because of the large clutch sizes of many animals in which most offspring die before maturity. The second shift that occurs as the number of organisms who fail increases is that each failing organism experiences a lesser degree of suffering. That is, in studying the inequality $nS > E$, the value of S goes down relative to E. Because these two effects go in opposite directions, as the number of failing organisms rises, total suffering may come to exceed total enjoyment, or the opposite may occur instead.

Ng (1995) recognizes this tradeoff as a kind of God-made fairness where animals in species more likely to fail experience relatively less suffering in each case of failure. That is, the more likely an organism is to suffer, the less relatively severe the suffering becomes. This happens because evolution seeks to minimize the costs of suffering and enjoyment, so the more cases there are of suffering, the less evolution invests in suffering relative to enjoyment. Ng (1995) surmises that there will still be more suffering than enjoyment in nature because the relative reduction in suffering will be too small to outweigh the probability of succeeding rather than failing. In fact, this intuition is inaccurate. The inequality can go either way depending, as stated above, on form of the evolutionary production function.

Remarkably, empirical observation of nature appears to match the predictions of this evolutionary model. The mathematical trade-off between the number of individuals suffering and the degree of each individual's suffering may be reflected in the nature of *r*-selected species. While mammals such as humans may not produce large numbers of offspring who die before reaching maturity, many organisms do produce large clutches, sometimes as many as thousands or tens of thousands (Horta 2010a), the vast majority of whom die shortly after birth of starvation or predation. While these organisms suffer in large numbers, they typically live relatively short lives, often extremely so. If indeed evolution is optimizing as described above and in Ng (1995), then this shorter lifespan may serve to attenuate the suffering.

Observation of nature, then, confirms the tradeoff underlying the revised premise. Where organisms suffer in large numbers, they seem to suffer relatively less based both on theoretical and empirical reasoning. This does not tell us whether the total amount of suffering by *r*-selected animals or in nature as a whole exceeds enjoyment, or vice versa. What it does tell us is that there is a tradeoff, and this tradeoff seems to be able to go either way. The revised proposition gives a precise condition for when we should expect suffering or enjoyment to predominate. Until further information is available, the economics of evolution are agnostic as to the net welfare of wild animals.

An illustration of suffering dynamics

While further research is necessary to fill in the evolutionary model for wild-animal welfare, psychophysics, biology, and even economics suggest that the evolutionary cost function may be logarithmic. Positing a logarithmic evolutionary

production function for suffering and enjoyment gives a picture of how the net balance of suffering and enjoyment may vary with the ratio of failure to success. With a logarithmic function, whether suffering or enjoyment predominates is ambiguous and again requires further empirical research. Calculations based on a logarithmic function suggest that, all else equal, larger organisms or those with more intense sentient experience may experience relatively more suffering and less enjoyment than smaller ones or those with less intense experiences. The effect of the rate of reproductive success on the balance of suffering and enjoyment can be positive or negative depending on organism size or intensity of consciousness.

One reason to think that the evolutionary production function for suffering and enjoyment may be logarithmic comes from the psychology of perception. The Weber–Fechner law in mathematical psychology states that perception of change in a stimulus is typically proportional to the size of the stimulus (Luce and Eugene 1963; Krueger 1991; Dehaene 2003). One experiment presents subjects with lines of different lengths and asks subjects to determine which line is longer or if both are equal. When the lines are sufficiently similar in length, respondents do not notice the difference. This is known as the "point of subjective equality" (Sugita and Suzuki 2003). When this experiment is run, the longer the lines, the larger the difference in length needs to be for subjects to notice it. In other words, while the difference between a 10-cm line and an 11-cm line may be perceptible, the difference between a 100-cm line and a 101-cm line is not. Perception of differences appears, based on most research, to be logarithmic: the difference between 10- and 11-cm lines is as noticeable as the difference between 100- and 110-cm lines or the difference between 1- and 1.1-m lines.

The physical production of suffering seems analogous to the production of awareness in response to a stimulus, and some further reasoning further supports the intuition that the two phenomena should share a similar form. Accurately perceiving stimuli in a lab is goal-oriented behavior, as participants typically want to get the answer right. Perception in that setting should therefore be mediated by the evolved reward mechanism. If the evolutionary reward function is logarithmic, the response to a stimulus should indeed be logarithmic. Furthermore, unconstrained by evolutionary resources, it would be optimal to be able to accurately perceive any difference in stimuli, so any limitation in human responses to stimuli should strictly reflect the evolutionary costs of perception. Given that suffering and enjoyment are forms of perception, the function for the production of suffering and enjoyment should follow a similar form to the function for reactions to stimuli. This gives some reason to posit that the evolutionary suffering function is logarithmic.

Evidence on self-reported responses to changes in income supports the use of a logarithmic function for suffering. Behavioral economists report that subjective life satisfaction increases logarithmically with income (Stevenson and Justin 2008). This does not necessarily show that happiness itself increases with log income. For example, responses to well-being questions may not adequately capture happiness on a daily level. Similarly, richer and poorer individuals may answer happiness surveys in systematically different ways that are distinct from real happiness. Still, Stevenson and Wolfers' finding is at least what we would

expect to see in a world where the production of suffering and enjoyment scales logarithmically with respect to the evolutionary costs. In conjunction with the evidence from the psychology of perception, this is suggestive, though far from confirmatory, of logarithmic evolutionary costs of enjoyment and suffering. For this reason, it is useful to posit a logarithmic cost function and study its implications, if only as an illustration of the evolutionary economics of wild-animal wellbeing.

Taking the production function for suffering and enjoyment as logarithmic, we can mathematically examine the net balance of suffering and enjoyment that would exist in nature and reach some secondary conclusions. The first conclusion is that even with a specific common function for the evolutionary production of suffering and enjoyment, it is not possible to say whether total suffering exceeds total enjoyment in nature in the absence of additional information. Let us take $E(C_E)$ and $S(C_S)$ as before and set $E(C_E) = \ln(\alpha C_E + 1)$ and $S(C_S)$ similarly for some $\alpha > 0$. Then the function $E(C_E)$ only meets the conditions for suffering to exceed enjoyment when $C_E > \frac{e-1}{\alpha}$. Since $C_E \neq C_S$, the actual point where the suffering overtakes enjoyment and vice versa will vary. In general, what we can see is that the logarithmic curve behaves differently with respect to the conditions in the revised Buddhist Premise at different parts of the curve, so even with this added specificity, it is still ambiguous whether suffering or enjoyment is in greater total abundance.

Setting an evolutionary budget for the production of suffering and enjoyment yields some insight into the relationship between suffering, failure rates, and intensity of experience. Suppose that an organism's genes can only afford a fixed amount of resources for the production of suffering and enjoyment, say M, so that $C_E + nC_S = M$, where n is the number of failing organisms per successful one.[3] If we take $E(C_E)$ and $S(C_S)$ as above and optimize under the new constraint,[4] the net excess of suffering over enjoyment, $S(C_S) - nE(C_E)$ is equal to:

---

[3] In the original paper (Ng 1995), n was defined as the number of failing organisms per successful organism, but this leads to a problem in the interpretation of a budget of the form $C_E + nC_S = M$. As n increases, two different attributes of the species increase: the failure rate and the total number of organisms whose costs are included by the budget. When $n = 5$, for example, the constant budget must be divided over six organisms. This is a problem, because we are interested in the optimization for each individual organism. We can think of there being a probability p of an organism succeeding and $p - 1$ of an organism failing, so that $pC_E + (p - 1)C_S = M$. This simplifies to $C_E + ((p-1)/p)C_S = M$, so we can think of n as being equal to $(p-1)/p$, or the ratio of the rate of failure to the rate of success, with no loss of generality.

An alternative way of dealing with this problem would be to include a further parameter, say b, for the number of successful organisms constrained by the budget, as Dawrst (2009) does. This would give us $bC_E + bnC_S = M$. This leads to the same conclusions, as the equation simplifies to $C_E + nC_S = M/b$. Note that M/b is exactly what we have defined M as above: the evolutionary suffering and enjoyment budget for an individual organism. Hence we can safely define n as the ratio between failure and success, and M as the individual budget constraint.

[4] The optimization problem here is to maximize the total extent of affective emotions per organism, that is, $E(C_E) + S(C_S)$, subject to the posited constraint, $C_E + nC_S = M$. Ng (1995) argues that genetic selection maximizes the per-organism difference between enjoyment in the case of success and negative enjoyment in the case of failure, which is equivalent to the sum of enjoyment per reproductive success and suffering per failure.

$$\left(\frac{1}{n+1}\right) \ln\left[\frac{(\alpha M+1)^{n-1}(n+1)^{n-1}}{2^{n-1}n^n}\right] \tag{5}$$

As expected, the sign of this expression can go either way for integer values of $n > 1$. The figure depicts the balance of suffering and enjoyment with α normalized to 1. If $n = 1$, suffering and enjoyment are in balance, as is obviously the case based on symmetry alone. For higher values of n, as in the case of species where the majority of animals fail to reproduce, there is net suffering for sufficiently large values of M and net enjoyment for sufficiently low values of M. As is clear, not only the magnitude but also the direction of the effect of n depends on the value of αM. In fact, as n goes to infinity, expression (5) becomes:

$$\ln\frac{aM+1}{2} \tag{6}$$

This expression can be positive or negative depending on αM, so for any rate of reproductive failure, either suffering or enjoyment can dominate. The balance is ambiguous because of the tradeoff described in the previous section: as n increases, the number of suffering organisms increases, but evolution cannot afford to make failed organisms suffer as much.

Figure: Net Suffering per Individual with Logarithmic Returns
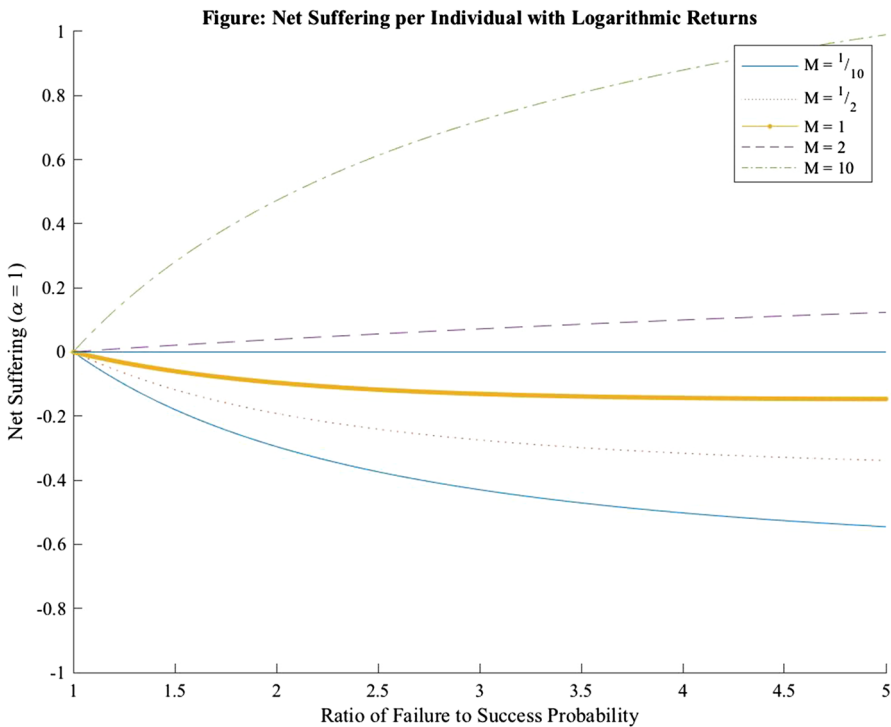
It is worth noting that as the evolutionary budget increases, the net balance of suffering and enjoyment shifts toward greater suffering. As M grows, expression (5) increases for all values of n, meaning that average suffering increases relative to enjoyment. For a sufficiently large value of M, average suffering exceeds enjoyment. It is unclear how to interpret the evolutionary budget M, but one way of interpreting it might be the intensity of sentient experience: the higher M, the more suffering and enjoyment the organism can experience. One might interpret M as representing the size of the organism, as organisms with larger neural structures may experience more intense experiences. This interpretation does not necessarily hold, though, because the logarithmic curve itself may vary based on organism size: that is, the parameter α may be smaller for larger organisms, as it may take more resources to make a larger organism experience pleasure given the organisms' bigger neurobiological structure.

Modeling the production of suffering and enjoyment as a logarithmic function of evolutionary resources offers one main lesson and a few secondary ones. Most importantly, it shows that identifying the parameters for the evolutionary optimization problem yield insight into the welfare of animals in the wild. Even with a family of functions identified, it still may be necessary to gather specific parameters on the evolutionary cost of suffering and enjoyment in order to appraise the state of nature. In addition, the logarithmic model tells us that under what may be the most plausible production function for affective experiences, greater intensity of experience leads to more suffering relative to enjoyment, while a higher rate of evolutionary failure relative to success has a surprisingly ambiguous effect. The logarithmic function offers hope that with further theoretical and empirical study to identify the correct equations, we can gather a more precise understanding of wild animal wellbeing as a function of animals' biological characteristics.

Toward empirical study of wild-animal welfare

Further refinements to the evolutionary model described above and in the earlier paper depend on progress in understanding the evolutionary reasons for suffering and enjoyment. Theoretical and empirical work on the neural correlates of wellbeing may shed light on the effect of natural selection on affective experience. The question of why animals evolved to feel pleasure and pain draws on work in evolutionary biology, neuroscience, and philosophy of mind. Answering the question likely involves addressing the aptly-termed "hard problem of consciousness," or the question of what physical processes give rise to phenomenal experiences (Chalmers 1995). On top of understanding the physical roots of consciousness, researchers would then need to determine the reasons why consciousness is evolutionarily adaptive.

Different evolutionary pressures for affective experience would imply changes to the model underlying the revised Buddhist Premise. For example, if the primary evolutionary advantage to emotions is mood regulation rather than subjective rewards for adaptive behavior, then the present model would not be as informative. If the main selective mechanism for emotions is how they help organisms focus (e.g.

on threats or opportunities for reproduction), we would need to look less at rates of failure and success and more at the relative frequency of situations where focus aids in reproduction. Ultimately it seems plausible that affective experience may serve multiple purposes, and a combination of models or a mixed model may be most instructive. Further research on the evolution of affective experience may yield new models of wild animal wellbeing or refinements to the current one.

Empirical research may be able to fill in the parameters in the appropriate model. Interpretation of the revised Buddhist Premise depends on what the actual evolutionary costs of suffering and enjoyment are. One possible "cost" for the production of suffering and enjoyment may be the resources needed to generate the neurotransmitters associated with suffering and enjoyment in animals' brains. Even here there is considerable complexity: while popular discussion fails to make such a distinction, positive mood and reward sensations have different neural correlates despite both being instances of what are commonly considered enjoyment or pleasure. The neurotransmitter known as dopamine appears to regulate motivation (Berridge and Robinson 1998), while the neurotransmitter serotonin appears to play a significant role in mood (Lesch et al. 1996). The neurotransmitter oxytocin has been associated with the distinctly positive (and evolutionarily adaptive) feeling of love, although it is more precisely associated with feelings of trust (Kosfeld et al. 2005). There is considerable difficulty in specifying the correct neurotransmitter or combination of neurotransmitters that must be created in a costly way to produce feelings. Furthermore, the evolutionary cost of suffering and enjoyment may lie in something else. Perhaps simply the energy cost or glucose needed to power the creation of neurotransmitters or energy in the brain acts as the relevant cost. It is also possible that the cost of suffering and enjoyment lies in something less material. Positive and negative feelings may have side effects or drawbacks that limit their use. They may overwhelm or distract an organism. Medication to address depression offers this theory some plausibility, as selective serotonin reuptake inhibitors do show some potentially evolutionarily relevant side effects, such as sexual dysfunction and weight gain (Waldinger et al. 1998; Maina et al. 2004). Given that, the evolutionary costs of suffering and enjoyment may not be material but rather tradeoffs with adverse side effects of affective states.

Progress on the evolutionary optimization problem also depends on valid measurements of wellbeing. Though the area is hotly debated, behavioral economists have made some progress in the past decade on measuring wellbeing in humans through carefully-constructed survey instruments (National Research Council 2014). Measuring wellbeing in animals is even more challenging. Much work in animal welfare measures wellbeing only in ordinal terms by looking at animals' preferences with regard to life attributes (Duncian 1992). One recent study supports observation-based measurement of cardinal wellbeing (Wemelsfelder et al. 2000). Other work suggests medical outcomes that are commonly associated with welfare, such as mortality and morbidity rates (Broom 1991). Still, these measures may indicate perception of or responses to wellbeing rather than wellbeing itself. This may be an important distinction. For instance, it may be the case that wellbeing does not follow a Weber–Fechner law, but self-assessed wellbeing does. In that case, survey respondents would only report differences in wellbeing that are large

relative to their overall level of wellbeing, given an inaccurate picture of their actual but difficult-to-describe emotional experiences. It may be useful to combine one or more of these measures with measures of brain activity to develop a more robust measurement of wellbeing, as some researchers have done with hedonic responses to taste (Berridge 2000). With enough research into the measure of wellbeing and the evolutionary costs of affective states, it may be possible to understand how the two relate and, therefore, what we should expect the state of wellbeing to be in the wild.

New directions on wild-animal welfare

In light of the revision of the Buddhist Premise, the common view in the academic and grey literature that suffering exceeds enjoyment in nature should be reconsidered. In the two decades since the publication of the original paper on welfare biology, a number of papers have discussed wild animal suffering, particularly in academic ethics (Cunha 2015; Horta 2010a, b, 2015; Dawrst 2009; Mannino 2015; Kymlicka and Donaldson 2011). In addition to the academic papers, a number of nonprofits have begun to focus on researching and potentially intervening in wild-animal suffering, including the Wild Animal Welfare Committee, Wild Animal Initiative, and Animal Ethics.

Both academic and nonprofit research on wild-animal suffering frequently cites the original implications of the Buddhist Premise. For example, Cunha (2015) cites Ng (1995) as support for the claim that the idyllic view of natural processes is false. Dawrst (2009) cites Ng (1995) as part of a paper claiming that there is likely to be more total suffering than enjoyment in nature and calls for further research on the subject. Horta (2010a, b, 2015) in turn cites Ng (1995) and Dawrst (2009) in making the same claim and in calling for intervention into nature where practicable. The research to date gives rise to a sense that caring about wild animal welfare necessitates a pessimistic view of nature. While the revised Buddhist Premise still does not offer support for the idyllic view of nature, it does retract support for a decidedly negative view of nature. Given this substantial correction to a key source, the academic and nonacademic literature on the subject of wild-animal welfare need an update toward a more agnostic view of whether nature is generally good or bad for its animal residents.

Given the ambiguity with regard to the goodness of nature, it may make sense for those concerned with animal wellbeing to promote research into wild animal welfare while supporting conventional views with regard to environmental conservation. If the wellbeing of animals in nature is ambiguous, it makes sense to base one's views on environmental issues on the more known benefits (and costs) of nature for humans. Until more knowledge is available, the most promising way to assist wild animals is likely to be academic research into welfare biology. Of course, this does not preclude immediate measures to reduce the suffering of *farmed* animals at low costs on humans (Ng 2016a) and eventual assistance to wild animals in the long run.

Concluding remarks

We have shown that based on Ng's (1995) evolutionary model, whether total suffering exceeds total enjoyment or vice versa is as of this moment ambiguous. The answer to this ambiguity depends on specific and currently unavailable information about the evolutionary optimization involved in the creation of positive and negative emotional experiences. As enjoyment and suffering are subjective, it is very difficult to establish, so theories that tie the evolution of emotions to flexibility in behavior, as Ng (1995) does, or other observable characteristics are more amenable to objective study. Empirical research into the evolutionary costs of feeling suffering and enjoyment and better measures of hedonic states would offer information to help resolve this uncertainty. Further progress at the intersection of evolutionary biology and neuroscience would also help. Until then, researchers in the area of wild-animal welfare should likely shift somewhat away from the pessimistic view of nature put forward in the original paper (Ng 1995).

Given the revised Buddhist Premise, the net balance of suffering and enjoyment in nature could go either way, and we should be cautious to claim otherwise. Some have argued that the existence of *r*-selected animals who birth many offspring only to die shortly after birth implies that nature is dominated by suffering. The model underlying the Buddhist Premise allows that this may be true, and yet it may still be the case that enjoyment exceeds suffering. As the number of organisms suffering increases, the degree each organism suffers decreases under the model presented in this paper. Evolution puts relatively less weight on suffering, because suffering becomes more costly for genes in expectation the more organisms experience it. Given this tradeoff between number and degree of suffering, it is not possible to conclude whether suffering or enjoyment is more common in nature without further study. Given the paucity of papers examining the wellbeing proper of wild animals (as opposed to evolutionary fitness or mere survival), more research would help to illuminate this problem.

Appendix: Derivation of Eq. (5)

We derive Eq. (5) starting with the following maximization problem:

$$\max_{\{C_E, C_S\}} \ln(\alpha C_E + 1) + \ln(\alpha C_S + 1)$$

$$s.t. \quad M = \frac{1}{n+1} C_E + \frac{n}{n+1} C_S$$

This yields the Lagrangian:

$$L = \ln(\alpha C_E + 1) + \ln(\alpha C_S + 1) + \mu(M(n+1) - C_E - nC_S)$$

Leading to first-order conditions:

$$0 = \frac{\partial L}{\partial C_E} = \frac{\alpha}{\alpha C_E + 1} - \mu$$

$$0 = \frac{\partial L}{\partial C_S} = \frac{\alpha}{\alpha C_S + 1} - n\mu$$

Combining and rearranging terms gives:

$$C_E = nC_S + \frac{n-1}{\alpha}$$

Plugging this into the budget leads to the following:

$$M(n+1) = nC_S + \frac{n-1}{\alpha} + nC_S = 2nC_S + \frac{n-1}{\alpha}$$

$$C_S = \frac{M}{2n}(n+1) - \frac{n-1}{2n\alpha}$$

Combining this with the equation for C_E in terms of C_S, we get:

$$C_E = \frac{M}{2}(n+1) + \frac{n-1}{2\alpha}$$

Now we can calculate the balance of suffering and enjoyment by taking suffering minus enjoyment per individual:

$$
\begin{aligned}
&\frac{1}{n+1}(nS(C_S) - E(C_E)) \\
&= \frac{1}{n+1}\left(n \ln\left[\frac{M\alpha}{2n}(n+1) - \frac{n-1}{2n} + 1\right] - \ln\left[\frac{M\alpha}{2}(n+1) + \frac{n-1}{2} + 1\right]\right) \\
&= \frac{1}{n+1}\left(n \ln\left[\frac{1}{n}\left(\frac{M\alpha}{2}(n+1) + \frac{n+1}{2}\right)\right] - \ln\left[\frac{M\alpha}{2}(n+1) + \frac{n+1}{2}\right]\right) \\
&= \frac{1}{n+1}\left(\ln\left[\frac{1}{n^n}\left(\frac{(M\alpha+1)(n+1)}{2}\right)^{n-1}\right]\right) \\
&= \left(\frac{1}{n+1}\right)\ln\left[\frac{(\alpha M + 1)^{n-1}(n+1)^{n-1}}{2^{n-1}n^n}\right]
\end{aligned}
$$

References

Berridge KC (2000) Measuring hedonic impact in animals and infants: microstructure of affective taste reactivity patterns. Neurosci Biobehav Rev 24(2):173–198. https://doi.org/10.1016/S0149-7634(99)00072-X

Berridge KC, Robinson TE (1998) What is the role of dopamine in reward: hedonic impact, reward learning, or incentive salience? Brain Res Rev 28(3):309–369. https://doi.org/10.1016/S0165-0173(98)00019-8

Broom DM (1991) Animal welfare: concepts and measurement. J Anim Sci 69(10):4167–4175. https://doi.org/10.2527/1991.69104167x

Caraco T (1980) On foraging time allocation in a stochastic environment. Ecology 61(1):119–128. https://doi.org/10.2307/1937162

Chalmers DJ (1995) Facing up to the problem of consciousness. J Conscious Stud 2(3):200–219. https://doi.org/10.1093/acprof:oso/9780195311105.003.0001

Clark S (1979) The rights of Wild things. Inquiry 22 (1–4):171–188

Cowen T (2003) Policing nature. Environ Ethics 25(2):169–182. https://doi.org/10.5840/enviroethics2003 25231

Cunha LC (2015) If natural entities have intrinsic value, should we then abstain from helping animals who are victims of natural processes. Relat Beyond Anthropocentrism 3:51. https://doi.org/10.7358/rela-2015-001-cunh

Dawrst A (2009) The predominance of wild-animal suffering over happiness: an open problem. Essays on Reducing Suffering. http://citeseerx.ist.psu.edu/viewdoc/summary?doi=10.1.1.116.8646

Dehaene S (2003) The neural basis of the Weber–Fechner law: a logarithmic mental number line. Trends Cognit Sci 7(4):145–147. https://doi.org/10.1016/S1364-6613(03)00055-X

Donaldson S, Will K (2013) A defense of animal citizens and sovereigns. Law Ethics Philos 1:143–160

Duncian I (1992) Measuring preferences and the strength of preferences. Poult Sci 71(4):658–663. https://doi.org/10.3382/ps.0710658

Ebert R, Machan TR (2012) Innocent threats and the moral problem of carnivorous animals. J Appl Philos 29(2):146–159. https://doi.org/10.1111/j.1468-5930.2012.00561.x

Gossen HH (1854/1983) The laws of human relations and the rules of human action derived therefrom. MIT Press, Cambridge, English translation of the 1854 original

Harsanyi JC (1953) Cardinal utility in welfare economics and in the theory of risk-taking. J Polit Econ 61:434–435. https://doi.org/10.1086/257416

Harsanyi JC (1955) Cardinal welfare, individualistic ethics, and interpersonal comparisons of utility. J Polit Econ 63(4):309–321. https://doi.org/10.1086/257678

Horta O (2010a) Debunking the idyllic view of natural processes: population dynamics and suffering in the wild. Télos 17(1):73–88

Horta O (2010b) The ethics of the ecology of fear against the nonspeciesist paradigm: a shift in the aims of intervention in nature. Between Species 13(10):10. https://doi.org/10.15368/bts.2010v13n10.10

Horta O (2015) The problem of evil in nature: evolutionary bases of the prevalence of disvalue. Relat Beyond Anthropocentrism 3:17. https://doi.org/10.7358/rela-2015-001-hort

Kosfeld M et al (2005) Oxytocin increases trust in humans. Nature 435(7042):673. https://doi.org/10.1038/nature03701

Krueger LE (1991) Reconciling Fechner and Stevens: toward a unified psychophysical law. Behav Brain Sci 14(1):187. https://doi.org/10.1017/S0140525X0004855X

Kymlicka W, Donaldson S (2011) Zoopolis: a political theory of animal rights. Oxford University Press, Oxford

Lesch K-P et al (1996) Association of anxiety-related traits with a polymorphism in the serotonin transporter gene regulatory region. Science 274(5292):1527–1531. https://doi.org/10.1126/science.274.5292.1527

Luce RD, Eugene G (1963) Psychophysical scaling. Handb Math Psychol 1:245–307

Maina G et al (2004) Weight gain during long-term treatment of obsessive-compulsive disorder: a prospective comparison between serotonin reuptake inhibitors. J Clin Psychiatry 65(10):1365–1371. https://doi.org/10.4088/JCP.v65n1011

Mannino A (2015) Humanitarian intervention in nature: crucial questions and probable answers. Relat Beyond Anthropocentrism 3:109

Matthews D (2015) The world's most famous utilitarian on whether all carnivorous animals should be killed. Vox. https://www.vox.com/2015/6/18/8802755/peter-singer

McMahan J (2010) The meat eaters. The New York Times 19. https://opinionator.blogs.nytimes.com/2010/09/19/the-meat-eaters/

National Research Council (2014) Subjective well-being: measuring happiness, suffering, and other dimensions of experience. National Academies Press, Washington DC

Ng Y-K (1995) Towards welfare biology: evolutionary economics of animal consciousness and suffering. Biol Philos 10(3):255–285. https://doi.org/10.1007/bf00852469

Ng Y-K (2016a) How welfare biology and commonsense may help to reduce animal suffering. Animal Sent 7(1):1–10

Ng Y-K (2016b) Utilitarianism generalized to include animals: response to commentary on Ng on animal suffering. Anim Sent 1:19

Pratt JW (1964) Risk aversion in the small and in the large. Econometrica 32(1/2):122–136. https://doi.org/10.2307/1912743

Rankin CH et al (2009) Habituation revisited: an updated and revised description of the behavioral characteristics of habituation. Neurobiol Learn Mem 92(2):135–138. https://doi.org/10.1016/j.nlm.2008.09.012

Stephens DW (1981) The logic of risk-sensitive foraging preferences. Anim Behav 29(2):628–629. https://doi.org/10.1016/S0003-3472(81)80128-5

Stevenson B, Justin W (2008) Economic growth and subjective well-being: reassessing the Easterlin paradox. No. w14282. National Bureau of Economic Research. https://doi.org/10.3386/w14282

Sugita Y, Suzuki Y (2003) Audiovisual perception: implicit estimation of sound-arrival time. Nature 421(6926):911. https://doi.org/10.1038/421911a

Thompson R, Spencer W (1966) Habituation: a model phenomenon for the study of neuronal substrates of behavior. Psychol Rev 1(73):16–43. https://doi.org/10.1037/h0022681

Tomasik B (2016) Habitat destruction, not preservation, generally reduces wild animal suffering. https://reducing-suffering.org/habitat-loss-not-preservation-generally-reduces-wild-animal-suffering/

Tversky A, Kahneman D (1992) Advances in prospect theory: cumulative representation of uncertainty. J Risk Uncertain 5(4):297–323. https://doi.org/10.1007/BF00122574

Waldinger MD et al (1998) Effect of SSRI antidepressants on ejaculation: a double-blind, randomized, placebo-controlled study with fluoxetine, fluvoxamine, paroxetine, and sertraline. J Clin Psychopharmacol 18(4):274–281

Weber EU, Shafir S, Blais A-R (2004) Predicting risk sensitivity in humans and lower animals: risk as variance or coefficient of variation. Psychol Rev 111(2):430. https://doi.org/10.1037/0033-295X.111.2.430

Wemelsfelder F et al (2000) The spontaneous qualitative assessment of behavioural expressions in pigs: first explorations of a novel methodology for integrative animal welfare measurement. Appl Anim Behav Sci 67(3):193–215. https://doi.org/10.1016/S0168-1591(99)00093-3

Wild Animal Welfare Committee (2019) Who are the guardians of wild animla welfare? Conference program. Wild Animal Welfare Committee, Edinburgh