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The importance of considering age when quantifying wild animals' welfare

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ABSTRACT

Wild animals experience different challenges and opportunities as they mature, and this variety of experiences can lead to different levels of welfare characterizing the day-to-day lives of individuals of different ages. At the same time, most wild animals who are born do not survive to adulthood. Individuals who die as juveniles do not simply experience a homogeneous fraction of the lifetimes of older members of their species; rather, their truncated lives may be characterized by very different levels of welfare. Here, I propose the concept of welfare expectancy as a framework for quantifying wild animal welfare at a population level, given individual-level data on average welfare with respect to age. This concept fits conveniently alongside methods of analysis already used in population ecology, such as demographic sensitivity analysis, and is applicable to evaluating the welfare consequences of human interventions and natural pressures that disproportionately affect individuals of different ages. In order to understand better and improve the state of wild animal welfare, more attention should be directed towards young animals and the particular challenges they face.

Key words: wild animal welfare, cumulative welfare, life history, demographics, ageing

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I. INTRODUCTION

The welfare of domesticated animals has been studied extensively; there is a whole field of veterinary science dedicated to it (Dawkins, 2006; Broom, 2011). Attention has also been given to the direct welfare effects of some human actions on wild animals [e.g. forestry (Blumstein, 2010); roads (Cappa, Borghi & Giannoni, 2019)], as human impacts on the environment have begun to blur the distinction between domestic and wild. However, comparatively little attention has been given to the welfare of individual wild animals independently of the conservation outlook for the species to which they belong. Here, I use the term 'wild animal' broadly, to include all animals whose lives are not managed in detail by humans. This includes animals living freely in human-dominated environments, such as parks and urban spaces, but excludes pets, livestock, and animals kept in zoos. Thus, the state of being a wild animal depends on the current circumstances of individual animals and not on the history of their species. A key objective of the nascent fields of conservation welfare (Beausoleil *et al.*, 2018) and welfare biology (Ng, 1995; Soryl *et al.*, 2021) is to evaluate the quality of lives lived by wild animals in order to identify causes of poor welfare, as well as safe and tractable interventions to improve their welfare.

The philosophical underpinnings of investigations into wild animal welfare can vary widely, from practitioners who believe humans have a duty of care to all wild animals (e.g. Capozzelli, Hecht & Halsey, 2020), to those who feel we only have a negative duty to avoid harming wild animals with our actions, or those who only value welfare instrumentally in order to improve other conservation outcomes (e.g. Cooke & O'Connor, 2010). Nevertheless, each of these motivations can only be addressed if we have ways to measure and assess the welfare of wild animals. Yet, it is unlikely that we will be able to assess the outcomes of our actions on wild animal welfare by measuring the welfare of every affected individual. Therefore, to use welfare data effectively, we must identify ways of scaling it up to the population level.

One of the main ways in which individual welfare might be distributed over a population is by age. When considering wild animals, it is common to imagine healthy adults acting out the lifestyle to which their species has adapted. Unfortunately, this is not representative of what most animals experience; in many species, only a minority survive to maturity. Consider the example of the American black bear (*Ursus americanus*). These animals are capable of long adult lives with liberal access to food and socialization, yet many bears end their lives while still cubs through predation, malnutrition, disease, or even flooding of their natal dens (e.g. Alt, 1984; LeCount, 1987; Chomel *et al.*, 1998). Many more bears' lives end as subadults, during the period of vulnerability between the withdrawal of maternal care and their full maturation (e.g. Elowe & Dodge, 1989; Schwartz & Franzmann, 1992; Clark & Smith, 1994; Miller, 1994). Bears that reach adulthood may live long and seemingly contented lives; but of course, even adult bears are vulnerable to disease, injury, and anthropogenic threats like vehicle collision and hunting. To be born as a bear is to gamble on all of these outcomes.

A full understanding of wild animal welfare, then, must take into account the range of lifespans that occur among wild animals of the same species, and the varying levels of welfare an individual might experience as they mature. That is to say, a synthesis of animal welfare science and population ecology is needed. Herein, I will explain the need for and describe an approach that takes into account the different levels of welfare wild animals may experience over the course of their lives, helping to evaluate the consequences of human actions and natural pressures that disproportionately affect animals of different ages.

II. ASSESSING WILD ANIMAL WELFARE

The age at which an individual is most likely to die depends on life-history traits expressed by and inherited from their parents (De Magalhães & Costa, 2009; Healy *et al.*, 2019). For example, in species with extensive parental care, offspring mortality risk can spike during the period after parental care is withdrawn but before the young animal fully matures (e.g. gentoo penguin, *Pygoscelis papua*; Polito & Trivelpiece, 2008). Juveniles are protected and provided for and may engage in play or other socialization. However, when parental care is withdrawn, these same juveniles transition to subadulthood and may face a period of greater difficulty in acquiring food, increased threat from predators, and a lack of positive social interactions while they finish maturing. As surviving individuals progress through prime adulthood and into old age, they may experience further positive and negative changes of circumstance.

These conditions of threat, challenge and respite relate to important facets of animal welfare as conceptualized by multiple widely used models which ask, fundamentally, whether animals are healthy and whether they have what they want (Dawkins, 2003). The Five Domains model conceives of an animal's mental well-being as the product of their physical condition, behaviour (including socialization), access to quality food and water, and environment (including perception of security) (Mellor & Beausoleil, 2015; Mellor *et al.*, 2020) (Fig. 1). The model provides a classification scheme for threats to animals' welfare, such as malnourishment, lack of shelter, poor health, fear/distress, and lack of enrichment and socialization. The Five Domains have been widely applied to domestic animals, including farmed animals. However, the domains are also applicable to many wild animals (Harvey *et al.*, 2020).

An absence of threats does not guarantee that an animal will live a truly good life. Moreover, certain positive experiences an animal can have might compensate for some negative experiences (Mellor & Beausoleil, 2015). This is especially relevant for wild animals, for whom many negative experiences are unavoidable, as most lack protection even

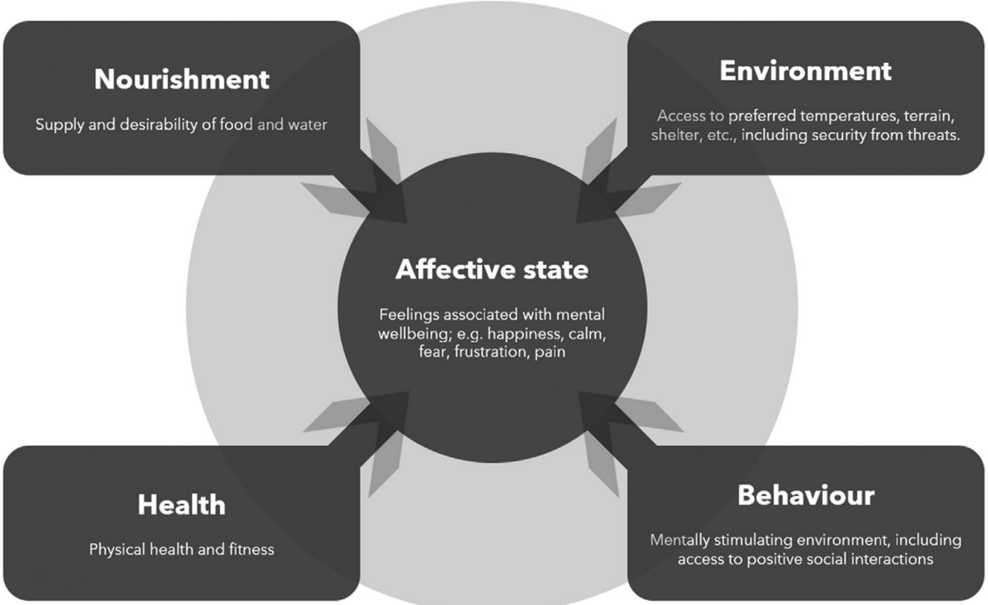

Fig 1. The quality of each of the four physiological domains (Mellor & Beausoleil, 2015; Mellor *et al.*, 2020) may vary with age in many species, amounting to changes in mental state and psychological well-being (affective state), together comprising the Five Domains model. Different scores in these domains may also affect individuals' lifespan, whether through immediate causes of mortality (dehydration, starvation, disease, overheating/freezing, or predation) or as chronic stressors impairing the immune system and accelerating ageing (Walker *et al.*, 2012; Bateson, 2016).

from the most basic causes of suffering, such as disease and hunger.

The welfare of wild animals as individuals has received relatively little research attention (Beausoleil *et al.*, 2018; Soryl *et al.*, 2021), in part because of the comparative difficulty of monitoring free-living individuals and the lack of a framework for systematically analysing their needs (but see Harvey *et al.*, 2020). While in-depth assessment of the welfare of each individual is clearly the ideal, this is unlikely to be tractable for most wild animal populations. In contrast to the closely managed lives of most domestic animals, especially those consigned to factory farms, wild animals' experiences can be incredibly varied. Given this variability, a degree of generalization will be required to scale individual-level welfare data up to be informative on the level of populations, species, and ecological communities. This sort of up-scaling is challenging, but with significant precedent in conservation science (e.g. landscape genetics; Storfer *et al.*, 2010). If individual welfare is indeed correlated with demographic characteristics, such as age or sex, obtaining a representative sample from which to generalize will require understanding a population's demographic structure.

Not enough is yet known about the precise factors determining individual welfare in most species to enable a proper welfare assessment based on the Five Domains model. In less well-understood species (or difficult-to-monitor populations of well-understood species), metrics such as body condition, biological ageing rate, stress hormone levels, and incidence of injury could be used to estimate welfare (Johnstone, Reina & Lill, 2012). For example, the healthiest individuals of these non-model populations could be used as benchmarks of good welfare. Of course, these are merely proxies and not a full substitute for a detailed knowledge of their behaviour, physiology and preferences. They should be respected as justifiable measures; a way to approximate wild animal welfare until new methods are validated and species-specific natural history knowledge is assembled.

III. WELFARE IS NOT CONSTANT

The daily probability of dying varies with age across nearly all populations (Healy *et al.*, 2019). The most likely manner of death also varies with age as a function of factors including self-sufficiency, disease susceptibility, socialization, and exposure to predation (Fig. 2). A meta-analysis of cause-specific mortality studies by Hill, Devault & Belant (2019*a*) suggests that predation accounts for almost twice as many juvenile deaths as adult deaths in mammals and reptiles, with adults being more affected by direct anthropogenic threats, like hunting. For example, Schmidt-Posthaus *et al.* (2002) found that juvenile Eurasian lynx (*Lynx lynx*) most commonly died from disease or starvation, while most subadults and adults died from disease or hunting, with some also dying as a result of accidents, including intraspecific fighting, falling and drowning. Birds, by contrast, showed relatively little difference between juvenile and adult causes of death (Fig. 2).

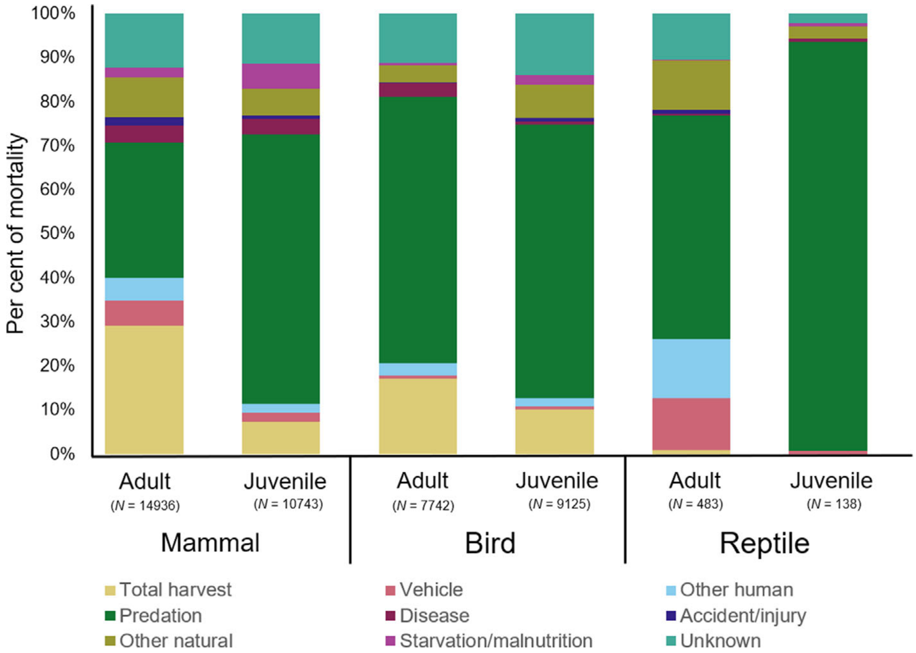

Fig 2. Cause-specific mortality rates separated by age and taxonomic class. Adapted from Hill *et al.* (2019*a*) based on data from the CauseSpec database (Hill *et al.*, 2019*b*).

The biological ageing process – senescence – is also expected to lead to an increasing incidence of intrinsic causes of mortality with age, as individuals' bodies gradually fail (Ricklefs, 2000; Carnes *et al.*, 2006; Moorad, Promislow & Silvertown, 2019). Siler (1979) modelled age-specific mortality rates as the product of competing risks that each varied in severity as a function of age. For example, in theory, a hazard of immaturity declines with age up to adulthood as individuals develop physically and learn to be self-sufficient, while adults of a certain age begin to suffer from the hazard of senescence, which increases over time. This approach has been influential on subsequent meta-analyses of cause-specific mortality data, especially in identifying effects of senescence on survival rates (e.g. Heisey & Patterson, 2006; Colchero *et al.*, 2019).

The fact that age-specific determinants of mortality rate (health, environment, social interactions, etc.) are closely related to widely recognized dimensions of welfare (Fig. 1) suggests that average welfare may also vary among age groups in a population as juveniles, subadults, reproductive adults and senescent adults often face different levels and forms of disease, competition, predation, socialization, and environmental hardship. For example, the scheduled withdrawal of feeding by parents thrusts their offspring into a stage of life during which they are more likely to die of starvation (e.g. chinstrap penguin, *Pygoscelis antarctica*; Moreno *et al.*, 1999). Presumably, individuals who are at elevated risk of starvation are also more likely to experience the feeling of hunger than they would be during other phases of life, even if they ultimately survive.

Relative age-specific mortality rates probably offer limited information about welfare in a given population. Specifically, they may reflect the frequency and/or severity of acute welfare threats, relative to the resilience of the affected animals (Rakotoniaina *et al.*, 2017). For example, if (in a hypothetical population) subadults have more encounters with predators than mature adults do over the course of a typical year, then even if subadults were equally capable of fending off predators, one would expect to see a higher rate of mortality among subadults, as well as an established cause of higher stress and poorer welfare (Clinchy, Sheriff & Zanette, 2013). The limits of age-specific mortality as a proxy for welfare are exposed by considering chronic challenges that may lead to premature death through illness or accelerated ageing, but never instantaneous death. These include most challenges related to the behavioural and environmental domains of welfare (e.g. social isolation), and some health challenges (e.g. malnutrition). Mortality rates are also unlikely to respond with adequate sensitivity to age-specific differences in exposure to positive stimuli, such as amicable social interactions, or food that is not only nutritious but varied and enjoyable. Some effect is expected, but it may only become apparent by comparing full lifespans (Walker *et al.*, 2012).

It is also conceivable that welfare might be invariant with age in some species, or that the determinants of welfare are so complex that welfare varies irregularly over a lifetime. However, it seems highly likely that welfare would shift in some direction concurrently with major life-history transitions, like the metamorphosis of a tadpole or caterpillar, the ejection of young male hyenas or female meerkats from their natal groups (e.g. Maag *et al.*, 2019), or sexual maturation in most species. Even in humans, whose welfare we may assume is determined by the most complex array of factors, clear age-specific patterns have been identified, such as a mid-life (age ~ 30–60) slump in happiness and life satisfaction, with peaks in early adulthood and around retirement age, and a gradual decline during late life (Cheng, Powdthavee & Oswald, 2017; Fig. 3). While many of the patterns associated with age-specific welfare in humans are functions of complex social effects, it is possible that common biological processes could also lead to sustained age-specific welfare patterns in wild animals. Such features of other species' typical lifetimes might be identified if more research was dedicated to quantifying their welfare. As with humans, though, the patterns and causes of welfare variation with age are likely to be specific to each population, summarising the diverse (but not entirely unique) experiences of its constituent individuals.

One of the best examples so far of welfare-relevant data for wild animals being broken down by age comes from the intensively monitored population of Seychelles warblers (*Acrocephalus sechellensis*) on Cousin Island (Hammers *et al.*, 2015). No single welfare indicator should be expected to provide a complete picture of an animal's affective state, as none can provide information simultaneously on all the Five Domains of welfare (Fig. 1). However, accelerated telomere attrition and aberrant haematocrit levels are expected to be linked to poor health and stress for a wide range of vertebrate taxa (Johnstone *et al.*, 2012; Filipsson *et al.*, 2017; Bateson & Poirier, 2019; Chatelain, Drobniak & Szulkin, 2020). These putative stress biomarkers [telomere attrition rate (Barrett *et al.*, 2013); haematocrit (Brown *et al.*, 2021)], as well as prevalence of malaria infection (Hammers *et al.*, 2016), have all been shown to vary with age in this population of Seychelles warblers (Fig. 4).

Brown *et al.* (2021) reported that juvenile warblers, in their first year of life, had very low haematocrit levels on average, but individuals at the upper end of their age-specific range of haematocrit values were found to have lower survival rates, possibly reflecting a physiological response to dehydration. Young, independent warblers (ages ~1–3 years) had higher haematocrit values than prime adults (ages ~4–7 years), which, the authors suggested, could indicate higher stress and demand for exertion during this stage of life, perhaps due to competition for territory and status.

Increased exertion during early independent life (i.e. subadult stage) has been widely reported, with different mechanisms proposed depending on the species. A common cause is foraging inexperience, with examples from some marine mammals and seabirds [e.g. Steller sea lion, *Eumetopias jubatus* (Trites & Donnelly, 2003); Galápagos sea lion, *Zalophus wollebaeki* (Jeglinski *et al.*, 2012); wandering albatross *Diomedea exulans* (Fay *et al.*, 2016); Cory's Shearwater, *Calonectris borealis* (Ramos *et al.*, 2019)]. For these diving animals, foraging efficiency is closely linked to physical development and stamina, putting immature individuals at a disadvantage. In

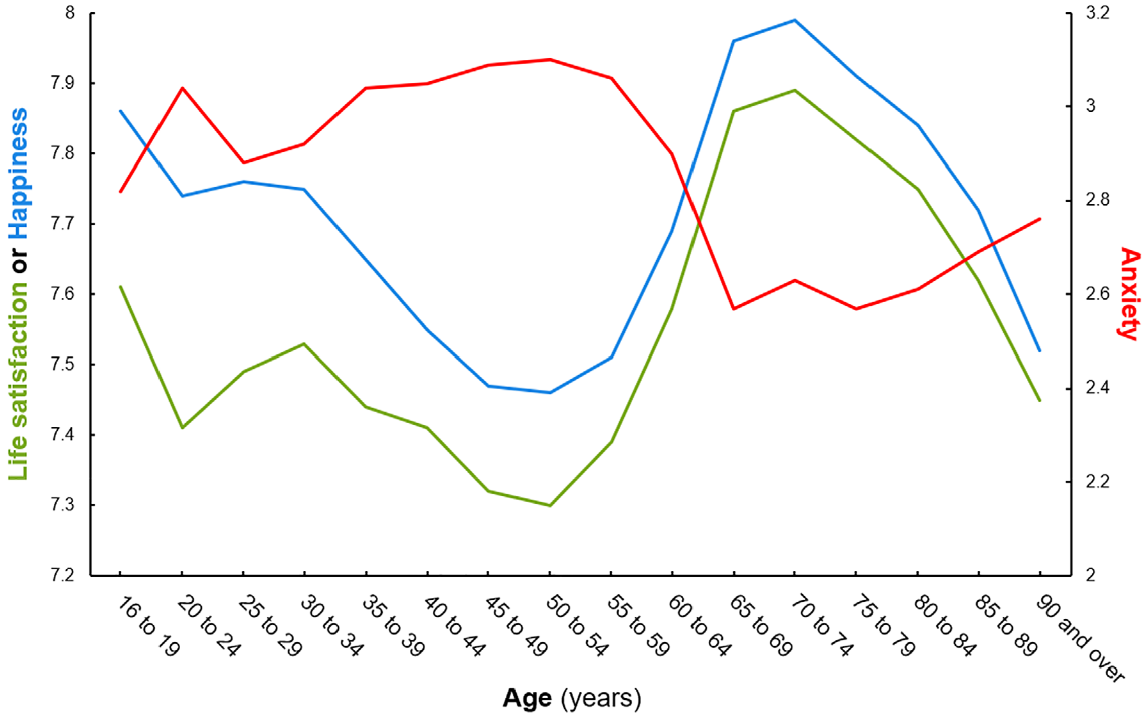

Fig 3. UK Office for National Statistics (2017) averages of happiness, life satisfaction and anxiety in men and women by age group, on a self-assessed 10-point scale. Similar patterns have been found in longitudinal studies, which avoid generational differences that might have confounded cross-sectional surveys like this one (e.g. Cheng *et al.*, 2017).

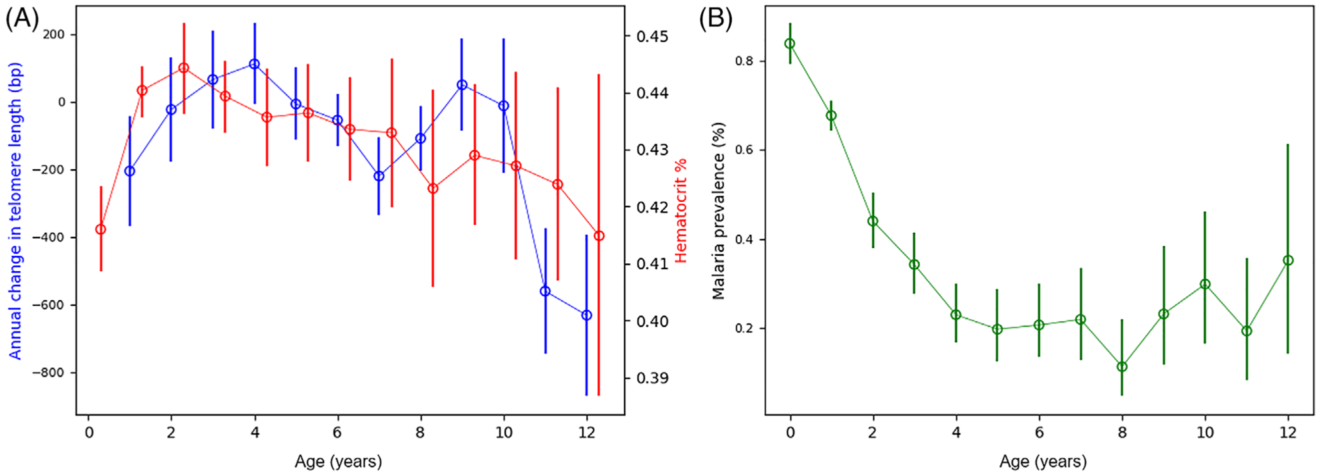

Fig 4. (A) Age-related trends in the mean values of annual telomere attrition rate (blue) and haematocrit (red) based on studies of the Seychelles warblers (*Acrocephalus sechellensis*) on Cousin Island (Barrett *et al.*, 2013; Brown *et al.*, 2021). (B) The prevalence of malarial infection varies strongly with age in the same population (Hammers *et al.*, 2016). Points and bars represent the mean ± standard error.

other taxa, low juvenile/subadult success relative to effort may result from other factors, such as suboptimal foraging strategies [e.g. savannah sparrow, *Passerculus sandwichensis* (Wheelwright & Templeton, 2003); bluegill, *Lepomis macrochirus* (Harrel & Dibble, 2001)], inability to compete with larger adults (e.g. grizzly bear, *Ursus arctos horribilis*; Keay, Robbins & Farley, 2018), or heightened need for predator avoidance [collared pika, *Ochotona collaris* (Holmes, 1991); turbot, *Scophthalmus maximus* and European flounder, *Platichthys flesus* (Nordström & Booth, 2007)] which may limit the foods and feeding sites available to subadults. Of course, not all aspects of welfare vary with age concurrently or in the same direction. For example, Granthon & Williams (2017) found that the heterophil-to-lymphocyte ratio (H/L), a common indicator of short-term stress in birds, was related to malaria prevalence in four species of songbirds. Contrary to their expectations, however, the authors did not identify significant age-specific differences in parasitaemia.

In some cases, differences in average welfare across juvenile, mature, and elderly animals may result from specific life-history adaptations. The concept of antagonistic pleiotropy has long been invoked to explain the evolution of ageing, where gene variants that are net beneficial to the reproductive fitness of an organism early in their life are selected for despite net-harmful consequences for the same organism later in life (Williams, 1957). This may help to explain the taxonomically common (but not universal) occurrence of poorer health late in life, possibly resulting in poorer welfare (Austad & Hoffman, 2018). However, it is also critical to remember that reproductive fitness does not always equate to welfare in the life of a single individual (Beausoleil *et al.*, 2018). As a result, the opposite trend can also occur, with life-history adaptations that increase lifetime reproductive fitness due to their benefits during adulthood, while plausibly reducing the welfare of juveniles. An example of this is found in the great crested newt (*Triturus cristatus*). In this species, local population density has opposite effects for juveniles *versus* adults (Cayuela *et al.*, 2019). Juveniles in crowded ponds experience lower survival rates and attain lower body size as a result of competition, while adults in crowded ponds experience higher survival rates due to the risk of predation being more thinly spread over the local population. Adults also receive a fitness benefit through more numerous mating opportunities. As a result, great crested newts approaching sexual maturity preferentially disperse in search of more crowded ponds, despite the consequences for juvenile survival and health.

IV. QUANTIFYING WELFARE ACCUMULATED OVER TIME

The importance of viewing welfare as something that accumulates over an animal's lifetime has been recognized in the context of animals used for food and experimentation (e.g. Green & Mellor, 2011; Pickard, 2013). Recently, Bateson & Poirier (2019) proposed that the ratio between biological and chronological age, as measured by biomarkers including telomere length, could be used as a proxy for the quality of welfare experienced across an animal's life, at least in many vertebrates. This approach is premised on the fact that cellular damage and repair is often triggered by physiological processes, the efficiencies of which can be affected by emotional states, such as stress or happiness (Bateson, 2016). For example, European starlings (*Sturnus vulgaris*) exposed to adverse conditions, such as sibling competition, have been shown to accelerate biological ageing over the study period, especially when they are weaker competitors (Gott *et al.*, 2018). An important caveat is that the magnitude of the effect of a given experience on the rate of ageing may not be in exact proportion to the subjective welfare impact of the experience. That is to say, something that is only mildly pleasant or unpleasant in terms of an individual's subjective experience could have an exaggerated or attenuated effect on metrics of biological ageing, depending on how directly it interacts (e.g. *via* somatic damage) with the physiological pathways that shape ageing biomarkers like telomere attrition and hippocampal volume (Bateson & Poirier, 2019). However, if further research continues to validate biomarkers of biological ageing as reliable welfare indicators for domestic animals, subsequent longitudinal studies of biological ageing in wild animals might be possible, with the goal of estimating the cumulative welfare contained in the lives of individuals with specific experiences and life outcomes relative to other members of their population.

The welfare value of a single year of life can be benchmarked in several ways depending on the intended application. Following the medical and welfare economics literature on quality-adjusted life years (QALYs) in humans (Weinstein, Torrance & McGuire, 2009), welfare could be expressed as a fractional value where 1 represents a year of life in ideal physical and emotional condition (including the complete absence of negative feelings such as hunger and loneliness). A direct adaptation of QALYs to domestic animals – welfare-adjusted life years (WALYs) – has been proposed by Teng *et al.* (2018), using surveyed opinions of veterinarians to apply impaired welfare weights to specific health conditions. For wild animals, this kind of analysis would be most appropriate in contexts and species where the preferences of individuals are relatively well understood. For example, Harvey *et al.* (2020) assessed the welfare of injured wild horses *Equus ferus caballus* using an ordinal scale based on the Five Domains model. If this approach was expanded to the entire local population of wild horses, it should be possible to build up a representative picture of their welfare and how it is structured in relation to age or other demographic categories.

V. ACCOUNTING FOR AGE-SPECIFIC VARIATION IN WELFARE AND SURVIVORSHIP

A focus on cumulative welfare requires understanding not only animals' moment-to-moment welfare, but also their lifespans, as lifespan determines the number and duration of positive or negative experiences individuals can have (Pickard, 2013). A population's demographic structure is conventionally represented by a life table noting, among other things, the proportion of a cohort that survive from birth to a given age ('survivorship'). From a survivorship curve, it is possible to calculate the proportion of the surviving cohort that die at that age ('age-specific mortality'), and the average number of years remaining to individuals of a given age ('residual life expectancy'). While life tables generally express their statistics in terms of proportions of a population or cohort, these proportions are equivalent to probabilities when down-scaled to the level of individuals. For example, from the perspective of a newborn, survivorship to age five represents their probability of living to at least age five.

Life expectancy from birth refers to the mean lifespan of individuals in a population. For example, a life expectancy of 3 years could mean that every individual lives for 3 years, or it could mean that two-thirds of individuals live for only 1 year while the remainder live 7 years. Life expectancy calculations weigh each year equally, since each year objectively represents an equivalent amount of time. However, as discussed in Section IV, different periods of an animal's life may contain different levels of welfare depending on the sum of welfare-relevant experiences during that period. If welfare varies with age, then individuals that die at different ages may have experienced different average levels of welfare over the course of their lives, as well as different total amounts of welfare (average welfare multiplied by lifespan). This potential for age-specific variation in welfare, against a background of variation in lifespan, calls for a distinct concept of 'welfare expectancy'.

I define welfare expectancy as the average sum of welfare that an individual born into a given population will experience over their lifetime. Many animals die as juveniles, only experiencing the level of welfare associated with that stage of life; more survive to adulthood, and some survive on to an advanced age. Each of these alternative biographies will clearly entail different amounts of time lived, but the average quality of welfare during those lifetimes may also differ. Individuals who die as young adults, for example, will have missed out on the welfare-relevant experiences of mating and parenthood, but will have experienced life as a juvenile, during which time they may have been especially vulnerable or effectively cared for (depending on their parents' life-history strategy). Individuals who survive beyond reproductive age will have experienced all of these stages, plus – in some species – a terminal decline in their health associated with senescence.

Welfare expectancy from birth (W_0) is calculated by summing the age-specific welfare values experienced over the ages encompassed by each possible lifespan weighted by the probability of that lifespan as derived from a life table or other demographic model. This is roughly equivalent to the equation for net reproductive rate, but with age-specific fecundity replaced with age-specific welfare (Stearns, 1992; Stubben & Milligan, 2007).

$$W_0 = \sum_{x=0}^{\omega} (d_x \times w_x) \tag{1}$$

where d_x = probability from birth of dying at age x, w_x = net total welfare experienced during a lifespan of x years, and ω = maximum lifespan.

The expected value of welfare in a 5-year life would equal the total welfare experienced by the average individual from birth to age five, multiplied by the probability of a 5-year lifespan. Repeating this operation for each possible lifespan and taking the sum would yield the welfare expectancy for an individual born into that population. For example, welfare expectancy in a bear population could be estimated as the average welfare of cubs multiplied by the average period of time spent as a cub (birth to family dispersal), plus the average welfare of subadults multiplied by the average duration of the subadult stage, and so on.

Considering how much uncertainty remains about the absolute levels of welfare experienced by most wild animals (Botreau *et al.*, 2007), it seems prudent to focus on relative differences in lifetime welfare among individuals of a given species. This can be expressed with a related metric, ‘demographic welfare expectancy’ (DWE), which asks whether the periods encompassed by the lifespan of the average individual in a population are above average or below average in terms of welfare, compared to an individual in the same population who lives out their full theoretical lifespan. For example, do most individuals only live long enough to experience the harshest times that life as a member of their species has to offer, while a privileged few survive to a relatively pleasant adulthood? To illustrate by reference to the human well-being data shown in Fig. 3, most people in the UK (life expectancy ~81 years) live through peaks and troughs of happiness and life satisfaction, the average of which is approximately representative of the well-being experienced over a maximum-length human lifespan (>100 years). By contrast, wild animals’ life expectancies from birth are typically less than 20% of their species’ theoretical longevity (Fig. 5). The great variability of lifespans within wild animal species demonstrates the potential for age-specific variation in welfare to lead to significant differences in the average welfare experienced over the course of individual animals’ lives, highlighting the need to consider age when assessing the welfare of wild animal populations.

The demographic welfare expectancy (DWE) index is calculated by normalizing age-specific welfare values (w_x) around 1, such that the sum of all w_x equals maximum lifespan ω. These values of w_x are then used to calculate welfare expectancy from birth (W_0) as in Equation (1). Finally, W_0 is divided by life expectancy (e_0): DWE = W_0/e_0.

This index quantifies the overlap of the average lifespan with periods of relatively high or low welfare. For example, a DWE > 1 implies that most individuals will live through periods of life characterized by above-average welfare, so average day-to-day welfare during the life of a typical individual would be greater than for an individual who lived out their theoretical maximum lifespan. On the other hand, for DWE < 1, a population’s survivorship patterns mean that below-average periods occupy a disproportionately large share of most individuals’ lifetimes. As life expectancy approaches a species’ maximum lifespan, DWE will tend towards 1 because the average welfare an individual experiences over the course of their lifetime is increasingly representative of average welfare over that species’ full theoretical lifespan. Whereas base welfare expectancy (W_0) scales with life expectancy, DWE does not; it is only affected by the relative age-specific distributions of lifespan and welfare, not by their absolute values.

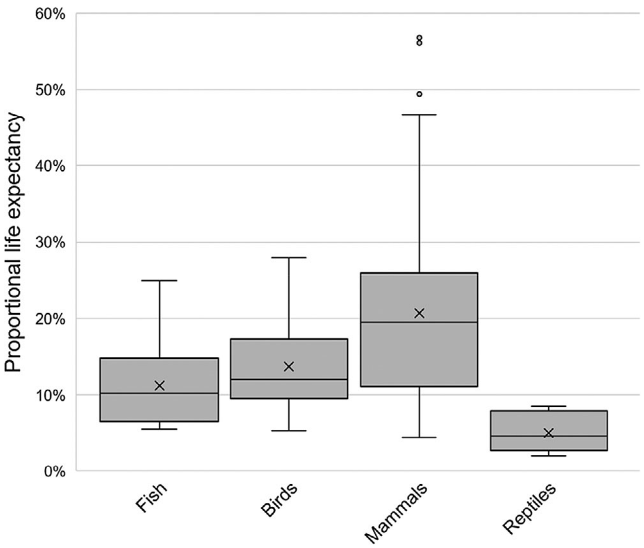

Fig 5. A boxplot showing life expectancy as a percentage of a species’ maximum lifespan for 152 populations of fish (N = 16), birds (N = 54), mammals (N = 72) and reptiles (N = 10). Each box encompasses the central 50% of the species’ proportional life expectancy estimates, the bars represent the top and bottom quartiles, and the circles are outlying data points. The horizontal line in the middle of each box denotes the median and the X denotes the mean. Most individuals live to only 10–30% of the age of the oldest known individuals of their species across these major vertebrate classes. Life expectancies were calculated from published models for wild populations, retained in the COMADRE database (Salguero-Gómez *et al.*, 2016). Maximum lifespans were obtained from the AnAge life-history database (De Magalhães & Costa, 2009).

VI. IMPLICATIONS OF AGE-STRUCTURED WELFARE

Many wildlife management strategies and conservation interventions influence the demographic structure of affected populations, intentionally or unintentionally. For example, demographic sensitivity analysis is sometimes applied to species to identify age groups for which a marginal reduction in mortality rate would result in the largest increase in population growth rate (Benton & Grant, 1999; Gerber & Heppell, 2004). This information then informs the design of conservation interventions like habitat reserves. An early use of this type of sensitivity analysis was in the evaluation of ‘headstarting’ programs for newborn turtles, where juvenile turtles are fed and protected until they are self-sufficient and large enough to have an increased chance of survival to adulthood. Demographic sensitivity analyses demonstrated that, despite the extreme juvenile mortality that is seen in some turtle species, small improvements to the survival of older turtles could actually have a greater effect on average lifetime reproductive output (e.g. yellow mud turtle *Kinosternon flavescens* and Kemp's ridley sea turtle *Lepidochelys kempi*; Heppell, Crowder & Crouse, 1996). But targeted protection of either juveniles or adults would also be expected to alter the equilibrium age structure of the species, just as would unequal exposure to threats (Holmes & York, 2003). For example, Monson *et al.* (2000) found that mortality among sea otters (*Enhydra lutris*) caused by the *Exxon Valdez* oil spill affected certain age groups disproportionately, skewing their population's demographic structure for generations after the event.

The mechanisms by which an intervention or management strategy can change age-specific mortality or reproductive rates to bring about a larger or demographically different population are also likely to alter the age-specific distribution of welfare levels by mitigating challenges (e.g. reducing disease mortality) or improving opportunities (e.g. providing better-quality habitat, such as shade for wildfire victims) for wild animals. Interventions like headstarting that aim to improve juvenile survival rates and welfare may be ideal for improving welfare expectancy in many populations, since nearly all individuals who are born would be eligible to benefit from such measures, which could improve the animals' immediate welfare as well as facilitating their survival to a self-sufficient age. The main reason that early-life interventions are arguably suboptimal in terms of population growth, yet seem plausibly ideal from the perspective of welfare expectancy, is that individuals of most species do not begin to reproduce until mid-way through their lives, but they may develop the capacity for welfare at a much earlier age.

It is a straightforward implication of the welfare expectancy approach that achieving good welfare in early life is most important, since by definition the entire cohort of each generation lives to experience their earliest stage of life. This reasoning can be generalized with a concept of age-specific welfare elasticity, asking at which age a proportional reduction in mortality rate would have the greatest impact on individuals' lifetime welfare expectancy by potentially extending their lives through periods of net-positive welfare. Demographic sensitivity analyses have become integral to wildlife population management as tools for designing the most effective interventions to increase net reproductive rate, or population growth rate (Gerber & Heppell, 2004). They have also been used less frequently to consider the sensitivity of life expectancy to changes in age-specific survival rates. For example, according to one study which drew on sparse data on the life histories of beaked whales (Family Ziphiidae), the life expectancy of beaked whales is most sensitive to changes in subadult survival, while their net reproductive rate depends most on the survival rate of mature adults (Chiquet *et al.*, 2015). The potential for age-specific variation in welfare would add another layer to these analyses.

The elasticity of welfare expectancy (s_x) to survival rate at age x is proportional to the product of the following terms: (*i*) the probability of surviving from birth to that age (l_x). Survivorship determines the proportion of individuals who would remain to benefit from an intervention to improve survival rates and/or welfare at a given age. (*ii*) The baseline mortality rate at that age (m_x). The probability that an individual would otherwise die determines the scope for improvement in survival rate. This reflects a practical assumption that major episodes or common causes of death may be more apparent and preventable, and therefore more effective targets for action to improve wild animal welfare (Manlik, Lacy & Sherwin, 2018). (*iii*) The expected value of welfare (W_{x+1}) in the remaining lifetime of an individual who survives that age. This represents the pay-off of an improvement in an age-specific survival rate.

For example, despite historically low rates of infant mortality, welfare expectancy among humans in the UK still appears most sensitive to improvements in the survival rate of infants (Fig. 6). Again, this makes sense given that every individual who is born experiences infancy, and so would benefit from interventions at that age, while individuals surviving infancy may go on to expect a long and relatively happy life on average. However, it is notable that lifetime welfare expectancy is only slightly less sensitive to proportional improvements in survival around retirement age. This is attributable to: (*i*) high reported levels of happiness among people of that age group; (*ii*) the population's high rate of survivorship up to old age, meaning that ~60% of individuals currently remain alive as late as age 80; and (*iii*) elevated baseline rates of mortality at this age, which leave much room for improvements in survival (i.e. high baseline mortality increases the magnitude of proportional reductions in mortality). These particular features of age-specific survivorship and welfare, such as having a 'retirement age', are clearly idiosyncratic to the studied human population. Yet, the same concepts could be applied to analysing any population for which similar data are available. Ages with especially high welfare elasticity can be thought of as 'bottleneck' ages, especially when they occur during later juvenile or subadult stages (e.g. following the withdrawal of parental care). Welfare bottlenecks can occur when (*i*) age-specific survival abruptly declines, having been (*ii*) preceded by high survivorship, and being (*iii*) followed by positive welfare expectancy. Bottlenecks occurring relatively early in life, when most of a cohort is still alive, may be promising targets for wildlife interventions, as improvements could benefit both biodiversity and welfare (Carslake, Townley & Hodgson, 2009) (Fig. 7).

Considering how small a proportion of their theoretical lifespan most individuals live through in many species (Fig. 5), the conditions for high welfare elasticity later in life may be uncommon. This suggests that all else being equal, interventions aimed at improving wild animal welfare may lead to the largest welfare increases when they benefit younger animals, since juvenile experiences will almost always be more numerous.

VII. OUTSTANDING QUESTIONS AND CHALLENGES

(1) Death as a discrete welfare event

Cause of death varies systematically with age in many wild animal populations (Fig. 2; Hill *et al.*, 2019*a*). Suppose that,

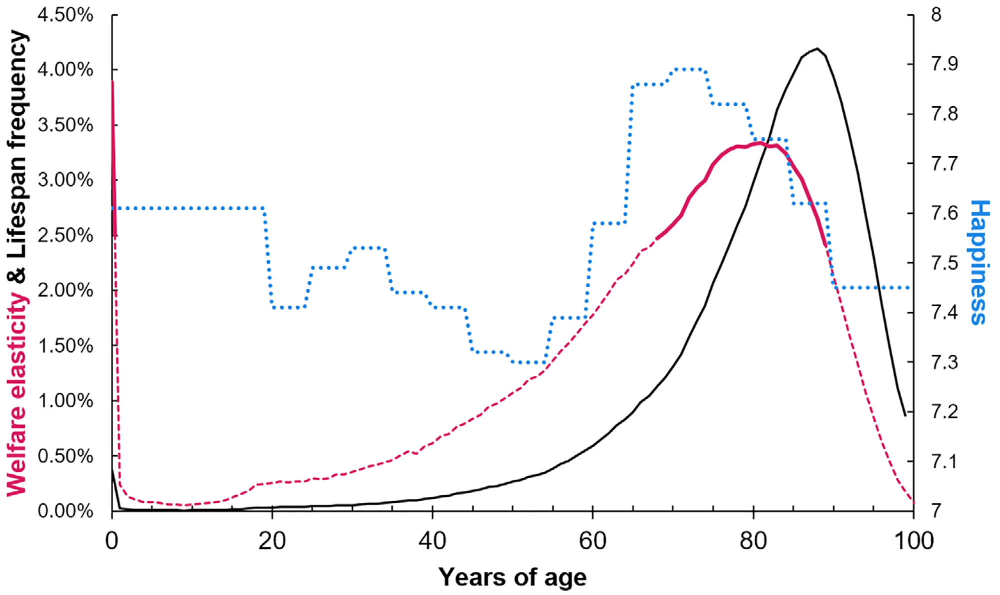

Fig 6. The confluence of age-specific mortality and age-specific welfare, illustrated here by the relative frequency of lifespans (black solid line) and self-assessed happiness on a 10-point scale (blue dotted line), determines how lifetime welfare expectancy can be affected by a marginal reduction in mortality rate at a given age (i.e. welfare elasticity; red dashed line). In this example based on UK census data for the human population (UK ONS, 2017), age-specific welfare elasticity is quantified as the per cent increase in lifetime welfare expectancy expected to result from a 10% reduction in annual mortality rate in the corresponding year of age. Welfare expectancy is found to be most elastic to such reductions in mortality rate during infancy and retirement (periods identified by red solid lines), with predicted benefits to lifetime welfare expectancy in excess of 2.5%.

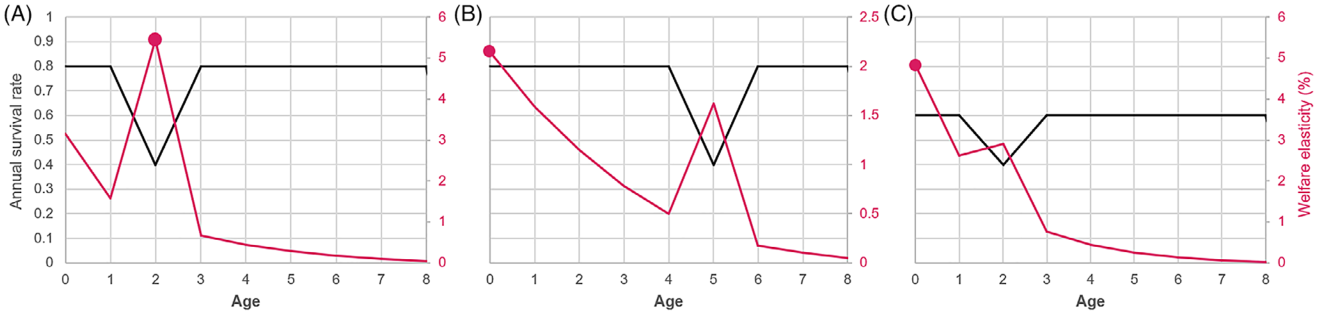

Fig 7. Age-specific survival rate (black) and corresponding welfare elasticity (red) for a hypothetical population where, for simplicity, age-specific welfare is assumed to be constant across age groups. The age at which welfare elasticity is highest is identified by a filled circle. (A) A scenario in which annual survival rate is high and constant (80%) except for a bottleneck during age 2, when the survival rate halves to 40%. As a result, lifetime welfare expectancy is most elastic to improvements in survival around age 2. (B, C) Welfare expectancy remains most elastic to the survival of the youngest age group despite this bottleneck if (B) the period of 40% survival is moved from age 2 to age 5, or (C) the constant survival rate is reduced from 80 to 60%.

in a hypothetical species, juveniles are most likely to starve while adults are most likely to be predated. If future research suggests that, for example, the suffering associated with dying of starvation is substantially greater than the suffering experienced during predation, then age-specific variation in the incidence of alternative manners of death and their severity could also be important factors in the lifetime welfare expectancy of individuals of this species.

Sharp & Saunders (2011) devised a scheme for expressing the relative severity of death in the context of animal culling methods, which has been adopted by other authors (e.g. Beausoleil *et al.*, 2016). Attempts have also been made to assess the severity of different causes of death in wild animals using physiological and behavioural indicators, with some studies revealing consistent differences in stress hormone levels associated with different causes of death, supporting the intuitive hypothesis that some involve greater suffering than others. For example, stranded right whales (*Eubalaena glacialis*) showed dramatically higher faecal glucocorticoid (fGC) concentrations than fishing gear-entangled whales, whose fGC concentrations were in turn dramatically higher than those of whales killed rapidly by a vessel strike (Rolland *et al.*, 2017). Similarly, red deer (*Cervus elaphus*) who were shot with a rifle showed lower cortisol levels than those hunted by dogs (Bradshaw & Bateson, 2000). Other studies have merely focused on the amount of time involved in the event leading to an animal's death (Hampton & Forsyth, 2016). Notably, these studies are all limited to different forms of killing by humans, which actually constitutes a small fraction of all wild animal deaths, even among terrestrial mammals, when juvenile mortality is considered (Ripple *et al.*, 2017; Hill *et al.*, 2019*a*). That being said, it is likely to be most feasible to improve the lives and deaths of animals already affected by human actions.

Previous authors have argued that for an animal to have had a 'life worth living', they must have experienced enough pleasure during their life to compensate for a potentially painful death (e.g. Green & Mellor, 2011; Scherer *et al.*, 2018). For animals able to live out most of their full lifespans, this seems highly plausible; but for the vast majority of animals, which experience only a small fraction of their potential lives, far more research into the causes and their experiences of death is needed to understand the overall summed emotional character of their lives.

(2) Comparing long-term and short-term welfare

A wild animal's welfare at any given moment may be shaped by both chronic and acute threats and opportunities (Mellor, 2016). The concept of welfare expectancy described in Section V provides a theoretical framework for integrating and comparing welfare over different timescales. However, this will depend on our ability to assess short-term and long-term welfare on a common scale in practice. This is challenging because, to assess the welfare impact of experiences that occur on different timescales, it may be necessary to use different welfare indicators that are appropriate to each timescale. This is especially true when dealing with acute stressors that cause the death of the animal. For example, an extremely traumatic minute – followed by death – is unlikely to be reflected in measurements of the deceased animal's telomeres, but may be registered by other welfare indicators, like behaviour or stress physiology. On the other hand, an animal with a relatively mild long-term illness (e.g. a deer carrying ticks) or living in a suboptimal environment may show only slight welfare impairment; too small to detect amid the background variability in available welfare indicators, but potentially reflected in their biological ageing rates over multiple years [see Gormally & Romero (2020) for a review of appropriate timescales for different stress indicators]. Another approach could be to rely on veterinary judgement about the moment-to-moment quality of life impairment attributable to a given condition or injury (as in Teng *et al.*, 2018) and multiply this by its duration to enable a rough comparison.

One advantage of taking a population-level perspective on individual welfare is that events that seem sudden and acute on an individual level may turn out to be less isolated given a larger sample size. As suggested earlier, a period when animals are more likely to die of starvation is probably also a period when more of them are experiencing hunger. For example, one individual dying from a disease or predation may leave behind dozens of conspecifics who suffered from the same disease or were attacked by the same predators and survived. Studying the lasting effects of trauma on surviving individuals [e.g. *via* biological ageing (Bateson *et al.*, 2015); cognitive bias (Mendl *et al.*, 2009); stress physiology (Sheriff, Krebs & Boonstra, 2010)] could help clarify the experience of the deceased and put it into longer-term perspective against the ongoing lives of survivors.

(3) The plausibility of improving age-specific welfare

It may be challenging to act on findings about relative age-specific welfare, if only because of the progress of time. If a population of animals is found to experience higher welfare in a specific type of habitat, it might be relatively straightforward to provide that habitat for them. On the other hand, if we found that the same animals achieved the highest welfare as juveniles, it would be impossible and ultimately counterproductive to halt their ageing process. A more realistic response would be to learn more about why their welfare appears higher at this age, and thereby attempt to achieve similar conditions at other ages, such as by ensuring access to food and water during especially challenging periods (e.g. Brittingham & Temple, 1988) or protecting against disease (e.g. Hanlon *et al.*, 1998; El Khoury *et al.*, 2018; Hoyt *et al.*, 2019). Additionally, some age-specific differences in welfare might be due to zero-sum competition between age groups. For example, adult wild horses may have higher welfare because they can exclude young horses from watering holes. However, even in cases like this, harmful effects of competition might be mitigated through management strategies, such as the use of wildlife contraception to limit population density while ameliorating resource scarcity (Massei & Cowan, 2014). In species with high survivorship to adulthood, some welfare issues are intrinsically linked to ageing. It may ultimately be possible to reduce suffering related to illnesses and ageing for these animals, as we do for members of our own species.

VIII. PRIORITIES FOR FUTURE RESEARCH

(1) Early-life survival rates

The 'welfare expectancy' approach laid out herein implies that lifetime welfare expectancy for individuals in a population will depend most on the periods of life that most newborn individuals survive to experience. Therefore, understanding a population's survivorship curve can help to target animal welfare research on the most sensitive age groups. By definition, the shape of a survivorship curve is most strongly affected by survival rates early in life, since these limit the absolute effect size of survival rates at later ages. Unfortunately, juvenile and subadult survival rates are currently known less well than those of adults for most wild animals (Hill *et al.*, 2019*a*). This is partially due to methodological challenges which can be overcome, but which deserve extra attention given the likely importance of juvenile survival to wild animal welfare in general.

The core methodological challenge is the classic problem of unobserved states. Most research into survival rates has been directed towards a better understanding of population growth rates. As a result, many studies focus on measuring 'recruitment' to the adult population within their study area. In theory, a population's recruitment rate is a lower-bound estimate of survivorship to adulthood because it does not distinguish between individuals who die and those who may disperse outside of the study area. This same problem of accounting for dispersal also influences estimates of adult survival rates. Fortunately, it is possible to correct for this and estimate more accurate rates by combining spatial modelling and multi-state mark–recapture models (Gilroy *et al.*, 2012; Schaub & Royle, 2014). If we aim to improve – or at least to understand – wild animal welfare, more studies should adopt these sophisticated modelling approaches.

Another challenge arises when juveniles die or disperse from their natal site very early, before researchers even have an opportunity to register their birth (e.g. Frederiksen, Wanless & Harris, 2004). One approach to overcome this is to estimate the survival rate of the missing animals using a life-cycle model that incorporates available data on survival and reproductive rates for all other stages. By assuming a specified population growth rate (ideally grounded in other data), such a model can be used to solve for the survival rate of the missing early-juvenile stage. For example, Pike *et al.* (2008) used this approach to correct previous underestimates of the juvenile survival rates of numerous reptile species.

(2) Early-life welfare

In populations with high juvenile mortality – a pattern which appears to characterize the life history of most wild animals due to its correlation with high fecundity (Healy *et al.*, 2019) – lifetime welfare expectancy may depend primarily on the quality of life individuals experience as juveniles and subadults. There is already a general need for research into the welfare and needs of wild animals, but this implies that that research should prioritize methods and questions that apply to juveniles, all else being equal.

Biomarkers of biological ageing are promising tools for comparing the welfare of animals of matched ages over a period of time. However, to use these methods to study age-specific variation in welfare due to extrinsic factors would require a better, species-specific understanding of how the rate of change in ageing biomarkers (e.g. telomere length) may vary with age based exclusively on intrinsic factors. For example, the telomeres of juvenile starlings shorten more rapidly than those of adults simply due to rapid cell division in growing birds (Gott *et al.*, 2018). Coincidentally, this accelerated background rate may make telomeres especially useful for comparing welfare among juvenile starlings (or other species exhibiting similar telomere dynamics) because stressors that accelerate ageing act multiplicatively on this background rate, leading to much larger disparities in telomere length for a given welfare effect size.

(3) Efficient, non-invasive welfare indicators for wild animals

Methods to assess wild animal welfare at any age need to be cost-effective and cause as little stress as possible. To achieve cost-effectiveness, methods can rely on averaging over a large population sample, rather than needing to provide precise results for each individual. To cause minimal stress, methods should require little to no physical or sensory contact with an animal. Telomere attrition as a marker of biological age is relatively inexpensive per sample, although it requires some physical contact for obtaining a blood sample. Methods from animal agriculture and experimentation, such as grimace scales, might be adaptable to wild relatives of some captive animals, including mice and rats (Whittaker, Liu & Barker, 2021). There is also evidence that physiological effects of negative affective state can influence animals' vocalizations in complex, yet detectable ways [e.g. goats (Baciadonna *et al.*, 2019); pigs (Briefer *et al.*, 2019)]. It seems plausible that vocalizations recorded through animal-borne devices could be used to monitor wild animal welfare (Mcloughlin, Stewart & McElligott, 2019). Scat analyses, which are already favoured for non-invasive population genetics research (Zemanova, 2020; Steinmetz *et al.*, 2021), also have potential to be developed into useful indicators of wild animal health and welfare. For example, mice exposed to social stress exhibit an altered microbiome, with characteristic changes in the relative abundance of specific bacterial genera (Bailey *et al.*, 2011).

IX. CONCLUSIONS

(1) Considering welfare in the context of animal age could help us avoid unintended harms from actions that specifically affect animals during particular life stages, as well as drawing our attention to periods of life where actions to improve the survival rates or welfare of individuals within those age groups could have an amplified impact on their lifetime welfare.

(2) Most wild animals live for only a small fraction of their potential lifespans. Therefore, the welfare of healthy adults, who tend to be most visible, cannot be taken as representative. In most cases, interventions to improve wild animal welfare may be of the greatest benefit where they focus on the youngest individuals.

(3) Lifespan is a crucial parameter determining the cumulative welfare that an animal will experience during their life. However, the value of an additional year of life may not be constant if welfare varies with age. Analysing the age-specific elasticity of welfare expectancy, based on the demographics of a population and the welfare threats its members face, can identify exceptions to the general argument for prioritizing the youngest individuals.

(4) The study of wild animal welfare is at a very early stage. However, the development of longer-term physiological indicators of welfare (Bateson & Poirier, 2019) and new frameworks for integrating a variety of information into a holistic welfare assessment for individual wild animals (Harvey *et al.*, 2020) suggests that we may be on the cusp of progress in this field. As appropriate data sets emerge, there will be a need to extrapolate from the welfare of individual animals to learn something about the welfare of their population as a whole, and to predict how it may change in response to forces that disproportionately affect different age groups. The concept of welfare expectancy aims to address this by simultaneously considering variation in longevity and age-specific welfare within populations.

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