

Accounting for demography in the assessment of wild animal welfare

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Declaration of Interest

I have no competing interests to declare.

1 **Abstract**

2

3 Welfare is experienced by individual animals, but the quantity and average quality of welfare an
4 individual is likely to experience in their lifetime is bounded by population demography; namely,
5 age-specific survivorship and the ecological forces that shape it. In many species, a minority of
6 the individuals who are born survive to adulthood, meaning that the lives of those we observe in
7 nature are often unrepresentative of the typical individual born into their population. Since only
8 living animals are capable of experiencing welfare, lifespan is effectively an upper bound on the
9 amount of affectively positive or negative experience an animal can accrue. Life history
10 strategies that increase the probability of a long life are therefore more permissive of good
11 welfare; but even holding life expectancy constant, specific patterns of age-specific mortality
12 may enable a larger proportion of individuals to live through periods characterized by above-
13 average welfare. I formalize this association between demography and welfare through the
14 concept of welfare expectancy, which is applied to published demographic models for >80
15 species to illustrate the diversity of age-specific mortality patterns and entertain hypotheses
16 about the relationship between demography and welfare.

17

18

19 **1. Introduction**

20

21 The experiences of wild animals are extraordinarily diverse. Individuals of different species
22 occupy different habitats, consume different resources, and engage in different behaviors. Even
23 within species, animals' fortunes differ based on their relative fitness or due to chance events,
24 leading to differential survival or mating success. While life history strategies evolve to maximize
25 inclusive fitness, it is crucial to recognize that fitness and welfare are not the same (Beausoleil
26 et al., 2018). For example, a strategy which maximizes mean fitness may do so while increasing
27 the variance in outcomes among siblings, leading to reproductive success in adulthood for a
28 few, but short lives for most (Pettorelli and Durant, 2007). Even for a successful individual, high
29 evolutionary fitness need not imply good welfare, as sexual competition forces trade-offs
30 between reproduction and survival or somatic maintenance (Johnston et al., 2013).

31

32 A key objective of the nascent fields of conservation welfare (Beausoleil et al., 2018) and
33 welfare biology (Ng, 1995) is to evaluate the quality of lives lived by wild animals in order to
34 identify causes of poor welfare, as well as safe and tractable interventions to improve welfare.
35 Empirical evaluations of wild animal welfare, such as those based on stress hormone levels and
36 other veterinary techniques, have been carried out, though few are comparable between
37 contexts (Schwarzenberger, 2007). One of the most promising proposals to date is the use of
38 differential rates of biological aging as an indicator of lifetime cumulative welfare under different
39 conditions (Bateson and Poirier, 2019; Poirier et al., 2019). For example, social stress related to
40 brood size and social rank has lifelong fitness consequences in birds that appear to be
41 mediated by telomere attrition, a prominent biomarker of biological age (Boonekamp et al.,
42 2014; Nettle et al., 2015). More generalized application of these methods will require
43 hypotheses to test and a framework for prioritizing which populations to evaluate and which
44 groups of individuals within them to potentially aid.

45
46 A promising starting point is to reason from demographic patterns such as the distribution of
47 individual lifespans. This approach is compatible with a wide range of assumptions about the
48 causes and levels of wild animal welfare, since only living animals are capable of experiencing
49 welfare. Moreover, the quality of life experienced by a typical week-old animal is likely different
50 from that of a year-old animal due to changing levels of vulnerability to disease and predation,
51 competition with conspecifics, self-sufficiency, and senescence.

52
53 Demographic patterns are observed at the population level but experienced by individuals.
54 Population models can provide examples of potential demographics, and although no firm
55 conclusions about welfare can be drawn from interspecific comparisons given our uncertainty
56 about the preferences and experiences of most animals, we can use their diverse population
57 dynamics to probe the implications of different hypotheses for how welfare varies with age.

58
59 Here, I set out a framework for incorporating demography in the evaluation of wild animal
60 welfare based on the principle of expected value and formalize previously expressed intuitions
61 about the relationship between life history and welfare. I also illustrate this by application to
62 published matrix population models for 160 populations of >80 species and formulate working
63 hypotheses about welfare to be tested by future field studies.

64
65

66 **2. Methods**

67

68 2.1 Matrix population models

69 Matrix population models (MPMs) use matrix algebra to represent transitions between life
70 stages in a population (Caswell, 2001). They are widely used to infer populations' instantaneous
71 rates of growth, as well as for estimating vital rates such as survival and fecundity, and
72 conducting population viability analyses (Heppell et al., 2000). MPMs may be structured by age,
73 stage, or another trait, such as size. For the analyses described here, I used exclusively age-
74 based models to avoid any ambiguity around stage durations.

75
76 It is possible to calculate the expected distribution of lifespans among a cohort from the age-
77 specific mortality rates given by an MPM. Life expectancy is then calculated as the sum of the
78 probability of each possible lifespan multiplied by its length (Caswell, 2009). Annual survival
79 probabilities were assumed to be the product of equal daily survival probabilities, so individuals
80 dying during a given year were assumed to have lived through half of that year.

81

82 2.2 Welfare expectancy

83 Life expectancy from birth (e_0) represents the expected value of lifespan, with the "value" of
84 each possible lifespan being equal to its length, each additional year of life being weighed the
85 same. Calculations of generation time – the expected age of mothers – follow a similar formula
86 but allow ages to differ in value as age-specific fecundity varies. Welfare may similarly vary with
87 age, as juveniles, sub-adults, reproductive adults and senescent animals face different levels

88 and forms of disease, competition, predation and environmental hardship. This potential for
89 variation calls for a distinct concept of welfare expectancy.

90
91 Welfare expectancy from birth (W_0) is calculated by summing the age-specific welfare values
92 experienced over the ages encompassed by each possible lifespan, and then taking the mean
93 weighted by the probability of each lifespan: $W_0 = \sum_{x=0}^{\omega} (d_x \times w_x)$... where d_x = probability from
94 birth of dying at age x ; w_x = net total welfare experienced during a lifespan of x years; ω =
95 maximum lifespan. For example, the expected value of a 5-year life would be equal to the total
96 amount of welfare experienced between ages 0 and 5, multiplied by the probability of a 5-year
97 lifespan. Repeating this operation for each possible lifespan and taking the sum would yield the
98 welfare expectancy for a typical individual born into the population in question.

99
100 A relative welfare expectancy (RWE) index can also be calculated using values of w_x
101 normalized around one ($w_x = (w_x \cdot \omega) / \sum_{x=0}^{\omega} w_x$) to calculate welfare expectancy ($W_{0,R}$), and
102 then dividing welfare expectancy by life expectancy: $RWE = W_{0,R} / e_0$. This index expresses the
103 variability of lifespan in relation to periods of high or low welfare. An $RWE > 1$ implies that most
104 individuals will survive to experience periods of life characterized by above-average welfare,
105 while for $RWE < 1$, a population's survivorship patterns mean that most individuals will only
106 experience below-average periods of life. For $RWE > 1$, welfare can be said to be
107 'outperforming' life expectancy, as the average instantaneous welfare value during the lifetime
108 of a typical individual would be greater than for an individual who lived out their theoretical
109 maximum lifespan. In general, either high early-life survivorship/welfare (many individuals
110 experiencing the best years) or extremely low late-life survivorship/welfare (few individuals
111 experiencing the worst years) can yield a high RWE index. As life expectancy approaches the
112 maximum lifespan of a species, RWE will tend towards 1 because the average welfare an
113 individual experiences in their lifetime is increasingly representative of the welfare distribution
114 over their species' maximum lifespan.

115

116 2.3 Welfare elasticity analysis

117 An elasticity analysis was also applied to each population to see whether they differed in the
118 age at which a proportional reduction in mortality rate would have the greatest impact on
119 individual's lifetime welfare expectancy. The elasticity of welfare expectancy to each age's
120 survival rate was scored as the product of 1) the survivorship up to that age (l_x), 2) the mortality
121 rate at that age (m_x), and 3) the remaining welfare expectancy conditional on surviving that age
122 (W_x). The age with the highest elasticity score was considered the welfare 'bottleneck' age for
123 individuals of that population.

124

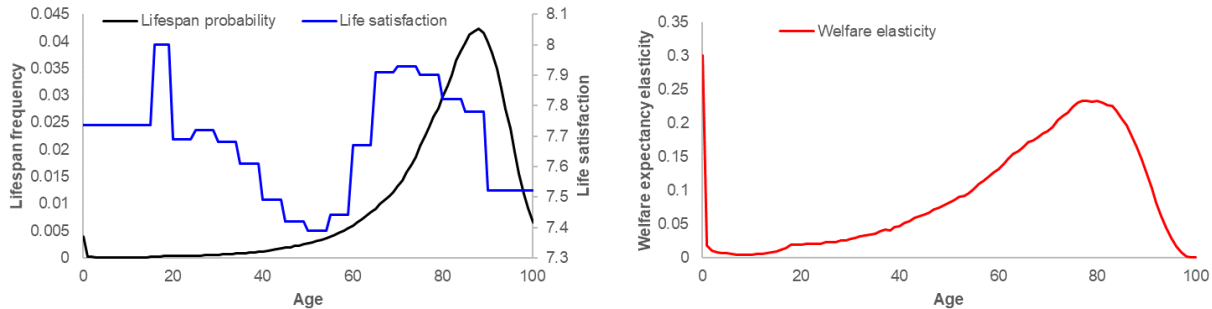
125 2.4 Illustrating the welfare expectancy approach

126 To provide an initial illustration of the approach described here using as detailed and explicit a
127 case as possible, a Leslie matrix was generated from age-specific rates of survival and welfare
128 (life satisfaction) among the human population of the United Kingdom, using published statistics
129 from the UK Office for National Statistics (ONS, 2016; 2019). This population was subjected to
130 the welfare expectancy analyses described above. It is so far unique in having empirically
131 determined age-specific welfare values, as well as vital rates calculated from known fates of

132 thousands of individuals, permitting the clearest possible illustration of the welfare expectancy
133 approach.

134

135



136

137 **Figure 1:** (Left) The lifespan distribution of UK humans plotted against age-specific welfare (life
138 satisfaction). Most individuals die old enough to experience both highs and lows of welfare
139 coinciding with important life transitions. (Right) Elasticity of welfare expectancy to marginal
140 reduction in age-specific mortality rate.

141

142

143 The UK human lifespan distribution begins with a modest spike representing infant mortality. It
144 then abruptly falls after the first year, rising again gradually from throughout senescent life
145 before spiking at 88 (Figure 1). The life expectancy at birth was approximately 80 years. Welfare
146 (life satisfaction) is bimodal, with peaks in the early-twenties (beginning of independent life) and
147 mid-sixties (beginning of retirement) and troughs in the mid-forties and old age. The population's
148 RWE index was 1.00, as the vast majority of individuals lived to old age and experienced
149 periods of high and low welfare in roughly equal measure (Figure 1, left). The age at which
150 welfare expectancy was most elastic to a marginal reduction in mortality was during year 1,
151 combating low but non-trivial infant mortality (Figure 1, right). This is to be expected given that
152 all individuals are alive and able to benefit from interventions at this age, and individuals
153 surviving infancy may expect a long and happy life. Notably, age 80 has only slightly lower
154 elasticity. This is because, although welfare expectancy from age 80 onward is much lower than
155 welfare expectancy from birth, the population's extremely high survival rates up to old age mean
156 that ~60% of individuals survive to benefit from interventions at age 80. Moreover, because the
157 age-specific mortality rate is much higher than during infancy, any intervention may have a
158 proportionally greater effect.

159

160 2.5 Modelling age-specific welfare

161 The distribution of welfare with respect to age is a crucial determinant of how changes in
162 demographic vital rates affect individual welfare expectancy, but there is yet virtually no direct
163 evidence on the age-specific welfare of wild animals. However, to explore the implications of
164 varying age-specific welfare, I assumed that welfare at a given age was proportional to the
165 probability of surviving that year of life. It must be stressed that this is a working hypothesis,
166 adopted for the purpose of illustrating the effects of age-dependent welfare under various real-

167 life demographics. The assumption remains to be tested, but its rationale, implications and
168 alternatives will be discussed later. Welfare expectancy specifically calculated under this
169 assumption will be denoted as $W_{0,s}$.

170

171 2.6 Data obtention

172 Published MPMs were obtained from the COMADRE database, which serves as a curated
173 repository for matrix population models (Salguero-Gomez et al., 2016). A subset of 152
174 population matrices, representing 88 species, were selected according to the following criteria,
175 in the form of variables defined in the COMADRE documentation: MatrixComposite == "Mean"
176 & MatrixTreatment == 'Unmanipulated' & MatrixCaptivity == 'W' & MatrixSplit == "Divided" &
177 ProjectionInterval == 1 & MatrixCriteriaOntogeny == 'No' & MatrixCriteriaSize == 'No' &
178 MatrixCriteriaAge == 'Yes'. Only the survival matrices ($\$matU$) were used. From this subset,
179 matrices were discarded if they had missing data ("NA" values), stage-specific transition
180 probabilities summing to >1 or to 0 at non-terminal stages or were duplicates. All MPMs were
181 annual Leslie or Leslie+ matrices (Carlslake et al., 2009). Original credit for these matrices goes
182 to their respective authors, as attributed in the COMADRE database.

183

184 Four major taxonomic classes were represented among the population matrices drawn from
185 COMADRE: Actinopterygii (ray-finned fishes), Aves (birds), Mammalia (mammals), and Reptilia
186 (reptiles). These were represented by 16, 54, 72, and 10 populations, respectively. Maximum
187 lifespans for each species was obtained from the AnAge database (De Magalhães et al., 2005),
188 if available, or else imputed as the average of represented congeners or family relatives. In the
189 case of Leslie matrices, the maximum lifespan was determined by the dimension of the matrix
190 itself. Statistics for each of these matrices can be found in appendix Table A1.

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193 3. Results

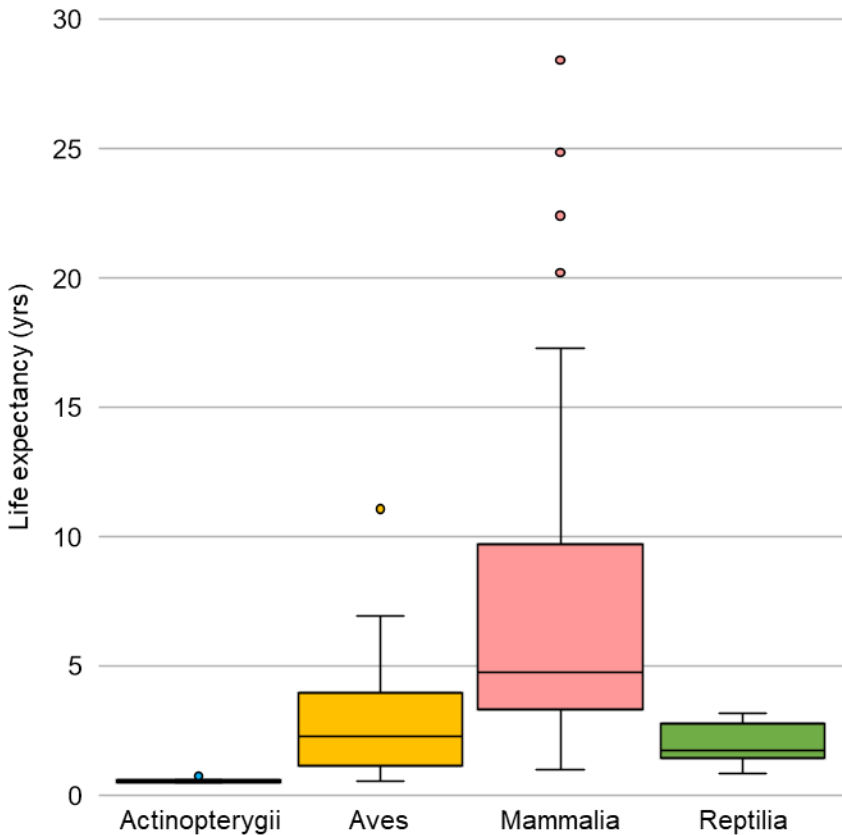
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195 3.1 Life expectancy

196 The mean life expectancy across the wild animal population models obtained from COMADRE
197 was calculated at 4.39 years, or a median of 3.14 years. Approximately 16% of populations had
198 life expectancies of <1 year, and 74% had life expectancies of <5 years. As a proportion of
199 maximum lifespan, the average life expectancy was 16%, with only 5% of populations having
200 life expectancies >33% of their maximum. Mammal populations had the highest average life
201 expectancy (6.8 years), followed by birds (2.8 years) and reptiles (2.0 years). The ray-finned fish
202 had the lowest average life expectancy, at 0.6 years (Figure 2).

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Figure 2: Box and whiskers plot of life expectancy by taxonomic class. Populations were used as data points.

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3.2 Welfare expectancy

211

The mean RWE index was 0.87, median 0.97. Only 10% of populations had relative welfare expectancies of >1.1, while 33% scored <0.9. Mammal and bird populations had RWE values typically near 1 (Figure 3). Mammalia had a tighter distribution around 1, consistent with the longer life expectancies of mammalian populations, but with positive and negative outliers.

214

Actinopterygii had by far the lowest mean RWE (0.20). Reptilian RWE values were intermediate, though all below 1 except for an extreme positive outlier (RWE=2.38) based on data from a population of painted turtles (*Chrysemys picta*) at E.S. George Reserve (Tinkle et al., 1981).

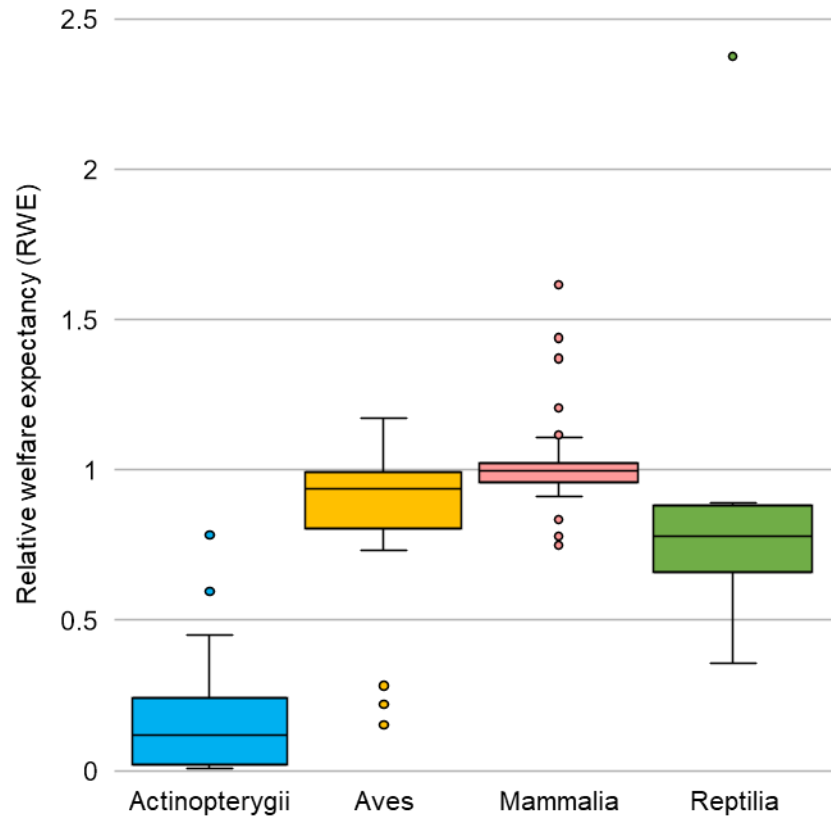
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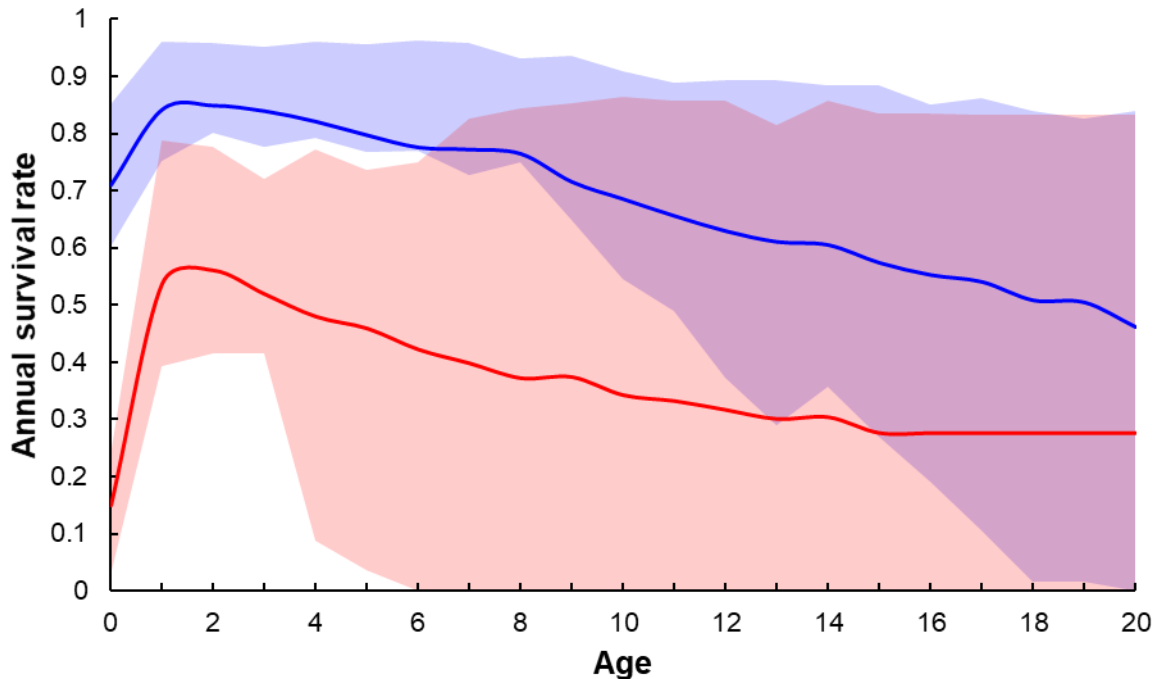
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Figure 3: Box and whiskers plot of RWE by taxonomic class, using populations as data points. The high-RWE outlier among Reptilia is a population of painted turtles (*Chrysemys picta*).

The average annual survival distributions of all populations with low (first quartile) and high (third quartile) RWE were plotted and found to cover distinct value ranges only during early life. High-RWE populations sustained a relatively high survival rate from birth onwards. Meanwhile, low-RWE populations had extremely low first-year survival rates, yet many attained higher survival rates similar to those of high-RWE populations by age 6 (Figure 4).



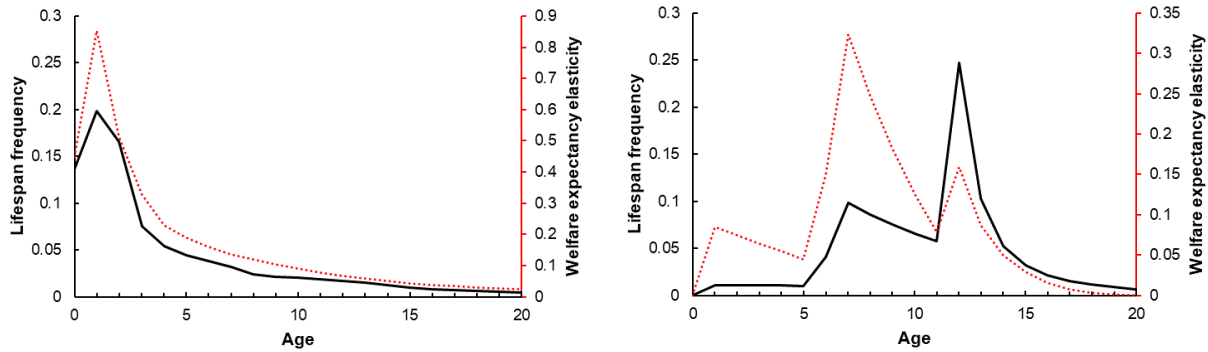
232
233 **Figure 4:** Mean age-specific annual survival rates for high-RWE populations (top 25%; blue
234 line) and low-RWE populations (bottom 25%; red line). Lighter blue and red bands cover the
235 interquartile ranges about each mean line. The purple area depicts overlapping age-specific
236 survival distributions of the high- and low-RWE groups.

237
238

239 3.3 Age-specific elasticity of welfare expectancy

240 The elasticity analysis identified only nine populations for which an infinitesimal reduction in
241 mortality rate after age 0 would lead to a greater increase in welfare expectancy than an
242 equivalent reduction in first-year mortality. For five of these populations, the age of highest
243 welfare elasticity was year 1 or 2, enabled by high survivorship over the preceding period
244 followed by a drop (the 'bottleneck'). The other four bottlenecked populations belong to the
245 same species, *Capra ibex*, and show a distinct lifespan distribution that leads to peak welfare
246 elasticity around age 7 or 12. In both cases, the elasticity of welfare expectancy to an age-
247 specific reduction in mortality parallels the lifespan distribution (Figure 5).

248
249



250
251 **Figure 5:** The lifespan distribution (solid black line) and corresponding age-specific welfare
252 elasticity (dotted red line) of five ‘bottlenecked’ populations with low age 0-1 survival but higher
253 age 1-2 and 2-3 survival (left) and four *Capra ibex* populations where welfare elasticity peaked
254 around age 7 or 12 (right).

255

256

257 4. Discussion

258

259 4.1 Life expectancy

260 Most of the individuals observable at any given time in many wild animal populations are the
261 lucky ones who have survived the challenges characteristic of early life. Among the populations
262 considered here, based on published demographic models, the typical life expectancy is merely
263 14% of the theoretical lifespan. While this is the median across populations, given that
264 predominantly shorter-lived taxa, such as the ray-finned fish, may produce far more offspring
265 per generation than longer-lived ones, the average life expectancy across individuals is likely to
266 be much smaller. The criterion of annual periodicity used for selecting population matrices from
267 COMADRE could further bias life expectancy upward, since an annual time-step would provide
268 poor resolution when studying a very short-lived animal. This is particularly relevant for
269 considering the lifespans of juveniles, which may encompass a fraction of one year.

270

271 Not all newborns of a given population will have the same individual life expectancies, after the
272 predictive power of parental phenotypes and circumstances of birth are taken into account.
273 Parental age, maternal body mass, clutch size, and relative timing of birth have often been
274 found to predict lifespan (e.g. Reid et al., 2010; Einum and Fleming, 2000; Tamada and Iwata,
275 2005; Ronget et al., 2018). Field research developing such predictors of individual differences
276 could help define life expectancy more precisely for subsets of a population, helping to target
277 interventions on the most vulnerable animals.

278

279 4.2 Age-specific welfare

280 Variation in lifespan also magnifies the relevance of differences in average quality of life with
281 respect to age among a given population. In a comparison of two populations with the same life
282 expectancy and theoretical lifespan, the one in which the largest proportion of individuals
283 survive to experience the most pleasant years of life available to them will have a greater
284 potential for net-positive welfare.

285

286 In the present analyses, I assumed that the welfare experienced at a particular age was
287 proportional to the probability of surviving that year of life. This is a plausible working hypothesis
288 since the same factors that lead to mortality (e.g. disease, vulnerability to predators, competition
289 for food) have been shown to lead to chronic stress and poor physical condition (Clinchy et al.,
290 2013; Bateson et al., 2015). Assuming this model of age-specific welfare, and equal life
291 expectancies, populations with a) very low mortality in early life followed by high mortality later
292 in life would achieve higher welfare than populations with b) a constant rate of mortality, and
293 these would in turn achieve higher welfare than c) populations with high early-life mortality but
294 high adult survivorship. These scenarios roughly correspond to the survivorship curve typology
295 of Demetrius (1978).

296

297 A number of alternative hypotheses might also describe the relationship between welfare and
298 age. For example, welfare might peak around the same age as peak reproduction. This could
299 occur due to hormonal factors, or simply because natural selection tends to optimize fitness
300 around reproduction, and body condition is likely related to welfare; though this might be
301 perturbed by intense juvenile competition or the need to provide protection for offspring, which
302 could drive peak physical fitness earlier or later than peak fecundity. On the other hand,
303 reproductive age might bring on poor welfare, especially in species with intense sexual
304 competition (e.g. Clinton and Le Boeuf, 1993). Either of these reproductive age-centric
305 hypotheses would likely still predict a correlation between survival and welfare, given the
306 interaction of age-specific mortality and reproductive timing in directing the evolution of life
307 history strategies (Charlesworth, 1980).

308

309 It is also conceivable that the determinants of welfare are so complex that welfare varies
310 irregularly over a lifetime, or average welfare might even be invariant with age in some animals.
311 If welfare is invariant with age, welfare expectancy will scale linearly with life expectancy.
312 However, it seems highly likely that welfare would shift in some direction concurrent with major
313 life history transitions, like the maturation of a tadpole or caterpillar, or sexual maturation in most
314 species, especially when this is accompanied by changes in environment, such as with the
315 ejection of young male hyenas or female meerkats from their natal groups (Maag et al., 2019).

316

317 Previous reviews have recognized the need to integrate welfare experienced over the lifetime of
318 domestic animals (e.g. FAWC, 2009; Pickard, 2013). The concept of welfare expectancy
319 developed here applies this to wild animal populations, using the principle of expected value to
320 account for their inherent variability. Recently, Bateson and Poirier (2019) proposed that the
321 ratio between biological and chronological age could be used as a proxy for lifetime welfare.
322 The premise of this approach is that somatic damage and repair, which determine biological
323 age, often result from physiological processes that are associated with affective states, such as
324 stress or happiness. Indeed, adverse conditions such as sibling competition have been shown
325 to lead to accelerated biological aging limited to the study period, especially when the individual
326 is a weaker competitor (Gott et al., 2018). Surveying population-level variation or tracking
327 individual longitudinal variation in the biological-to-chronological age ratio, through
328 measurements such as telomere length, could be a cost-effective way to estimate relative age-

329 specific welfare within wild populations. In the Anthropocene, a large proportion of wild animal
330 stress may be caused by human activity, and so biomarkers such as these could provide
331 evidence of habitat quality from the perspective of the animals themselves and serve as
332 additional holistic evidence to present policymakers (Wikelski and Cooke, 2006).

333

334 4.3 Welfare expectancy

335 Since only living animals are capable of experiencing any level of welfare, life expectancy has
336 profound implications for the net welfare of a population. I have defined welfare expectancy from
337 the perspective of an individual being born into a population and facing an uncertain lifespan.
338 Welfare expectancy revolves around age-specific variation in welfare and the implication that
339 some lifespans will encompass a greater quality and quantity of welfare than others. Many
340 animals die as juveniles, only experiencing the level of welfare associated with that stage of life
341 as a member of their species; others survive to adulthood but fail to reproduce, while others live
342 long, iteroparous lives.

343

344 The potential for age-specific variation in average welfare suggests that welfare expectancy
345 may 'outperform' life expectancy in populations where welfare is highest in early life, which most
346 individuals will live to experience. Conversely, in populations where juvenile welfare is lower
347 than adult welfare, welfare expectancy may 'underperform' life expectancy because most
348 individuals never see their best years. This notion drives the concept of relative welfare
349 expectancy (RWE). Assuming the correlation between age-specific survival and welfare argued
350 above, welfare expectancy in one third of the populations considered here underperformed their
351 life expectancy by at least 10% ($RWE < 0.9$), while only eight percent outperformed life
352 expectancy to the same degree ($RWE > 1.1$). Importantly, this conclusion was neither inevitable
353 nor universal. For example, in the study of *C. ibex* referenced earlier, not a single tagged animal
354 was found to have died during their first year (Toïgo et al., 2007). In contrast, the chinook
355 salmon (*Oncorhynchus tshawytscha*) had a first-year mortality rate of ~94% despite a
356 theoretical lifespan of nine years attained by a tiny proportion of individuals (Wilson, 2003).
357 Unfortunately, this second pattern appears to be more common, and is likely to be more
358 common in nature after taxon-related publication bias and differences in fecundity are taken into
359 account.

360

361 It should also be noted that RWE itself merely describes the natural state of a population. It can
362 inform population management as a descriptive statistic for prioritizing aid to particular
363 demographics within a population, as a low RWE indicates that something about the
364 population's age-specific survival pattern is out of order. However, the metric should not
365 necessarily be maximized by any possible means; for example, higher RWE could sometimes
366 be achieved by reducing late-life welfare as opposed to increasing early-life survival. Welfare
367 expectancy itself, which underlies RWE, should be maximized through population management.
368 However, the average welfare expectancy of individuals may need to be traded off against the
369 size of a population, as increasing density has potential to reduce both survivorship and welfare.

370

371 4.4 Welfare elasticity

372 A corollary of thinking about lifetime welfare in terms of expected value is the possibility of
373 'bottleneck' ages: ages where survival rate abruptly falls, which are preceded by high
374 survivorship and followed by positive welfare expectancy. This concept is analogous to
375 demographic elasticity, which is analyzed to identify which life stages and vital rates exercise
376 the most control over a population's marginal net reproductive rate (Benton and Grant, 1999).
377 Whereas age-specific demographic elasticity depends on the parallel dynamics of survival and
378 fecundity, welfare elasticity depends on an age's relation to patterns of survivorship and welfare.
379 In general, the value of increasing survival rate at a particular age depends on the proportion of
380 individuals in the cohort surviving to reach that age and their expectation of future welfare.

381
382 Bottlenecks occurring relatively early in life, when a respectable proportion of individuals remain
383 alive, may be promising objects for wildlife interventions from both a conservation perspective
384 accounting for both biodiversity and welfare (Carslake et al., 2009). However, because of how
385 few individuals of most species survive to adulthood, the conditions for a mid-life bottleneck
386 period to be the most sensitive target for intervention appear to be uncommon. Thus,
387 conservation interventions justified on holistic welfare grounds are likely to be most efficient
388 when they target younger animals, who will generally be more numerous. Calculations of the
389 expected value of any welfare intervention should account for the ages of individuals who would
390 be affected by the intervention.

391
392 A more precise understanding of these survival and welfare parameters could elaborate on
393 welfare expectancy through related statistical concepts, such as welfare skewness and
394 variability (c.f. Caswell 2009 for life expectancy). Variance in welfare would be particularly
395 important to understand if we prioritize solving cases of extremely poor welfare. If intraspecific
396 variation in welfare is structured by geography, phenology or phylogeny, it might also be
397 appropriate to study and manage the welfare of those groups separately, similar to how
398 demographically independent units are often managed separately for biodiversity conservation
399 (e.g. Höglund et al., 2011).

400

401 4.5 Death as a discrete welfare event

402 Previous publications have reasoned that for an individual animal to have had a 'life worth
403 living', they must have experienced enough pleasure during their life to compensate for a
404 potentially painful death (e.g. FAWC, 2009; Scherer et al., 2018). For animals who are able to
405 live out most of their full lifespans, this seems highly plausible; but for the vast majority of
406 animals, who experience only a small fraction of their potential lives, far more research into the
407 causes and their experiences of death is needed to understand the valence of their lives.

408

409 Cause of death, and therefore the duration and pain of an animal's experience of dying, may
410 also vary with age similarly to welfare, though probably less systematically. In a hypothetical
411 species, juveniles might be most likely to starve while adults are most likely to be predated, with
412 the relative probabilities of these and other mortality factors shifting over a lifetime. If future
413 research suggests that the pain of death is a sufficiently strong factor to negate some of the
414 positive welfare an animal might have experienced while alive, age-specific variation in the
415 incidence of various manners of death and their severity would also be important to account for.

416
417 It is already possible to assess the welfare state of an individual - and to compare individuals
418 within a species - using physiological and behavioral indicators. Several studies have
419 documented consistent differences in stress hormone levels associated with different causes of
420 death, supporting the intuitive hypothesis that some involve greater suffering than others. For
421 example, stranded whales showed dramatically higher fecal glucocorticoid (fGC) concentrations
422 than fishing gear-entangled whales, whose fGC concentrations were in turn dramatically higher
423 than those of whales killed quickly by a vessel strike (Rolland et al., 2017). Similarly, deer who
424 were shot with a rifle showed lower cortisol levels than those hunted by dogs (Bradshaw and
425 Bateson, 2000).

426 427 4.6 Conclusions and implications

428 The consideration of age structure when evaluating the overall state of welfare in a wild animal
429 population brings several general implications and heuristics. 1) Most individuals live only a tiny
430 proportion of their potential lifespans, so the welfare of healthy adults, who tend to be most
431 visible, is not representative. 2) As a consequence of this, interventions to improve welfare can
432 normally achieve greatest impact by focusing on the youngest animals. 3) Welfare and manner
433 of death are likely to vary with age, potentially disrupting or augmenting the focus on the
434 youngest animals. The ideal welfare scenario - within a fixed theoretical lifespan - is for as large
435 a proportion of animals as possible to live through the most pleasant years of life and die at the
436 age where the typical manner of death is the quickest and least painful. 4) Since only living
437 animals experience any welfare at all, life expectancy is a crucial factor in determining the scope
438 for positive or negative welfare. However, if welfare varies with age, the typical individual may
439 experience higher (or lower) net welfare than their relative life expectancy would suggest.

440
441 At the individual level, welfare expectancy unites two distinct concepts: the day-to-day quality of
442 welfare and quantity of welfare experienced over an individual's lifetime. However, a similar
443 quantity-quality distinction applies at the level of populations, with welfare expectancy
444 addressing the quality side of the argument and quantity being determined by the population
445 size. Management decisions should be based on the sum of welfare expectancy, but density
446 dependence of age-specific survival rates will in many cases lead to a trade-off between the
447 average and the sum of welfare expectancy in a population (assuming habitats do not grow),
448 implying the existence of an optimum density (e.g. Cubaynes et al., 2014). Understanding the
449 relative sensitivities of a specific population's vital rates to density is therefore crucial for optimal
450 welfare-centric management.

451
452 Once better data on age-specific welfare become available, the welfare expectancy framework
453 could also help wildlife managers to identify specific ages or stages to target for population
454 control where a reduction in survival rate would lead to the smallest possible change in welfare
455 expectancy for the largest possible reduction in net reproductive rate. Such compromises could
456 also be identified for growth-oriented population management, ideally achieving high individual
457 welfare among a large population.

458

459 The field of welfare biology is at a very early stage, having received little dedicated work from
460 the life sciences until recently. While progress is still limited by the lack of empirical studies of
461 wild animal welfare, it is hoped that this theoretical work, drawing on some of the same
462 published demographic data which are widely used for informing biodiversity conservation, will
463 help establish a paradigm for prioritizing and interpreting future research in welfare biology.
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603 **Appendix**

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605 **Table A1:** Core numerical results for each population from COMADRE included in the analysis.

606

| Class | Genus species | Max lifespan | Life expectancy | $W_{0,s}$ | RWE |
|----------------|---------------------------------|--------------|-----------------|-----------|------|
| Actinopterygii | <i>Ammocrypta pellucida</i> | 3 | 0.52 | 0.02 | 0.14 |
| Actinopterygii | <i>Astroblepus ubidiai</i> | 6 | 0.79 | 0.20 | 0.78 |
| Actinopterygii | <i>Cottus</i> sp. | 5.89 | 0.52 | 0.01 | 0.07 |
| Actinopterygii | <i>Erimyzon sucetta</i> | 6 | 0.50 | 0.00 | 0.01 |
| Actinopterygii | <i>Hybognathus argyritis</i> | 4.4 | 0.51 | 0.01 | 0.07 |
| Actinopterygii | <i>Notropis percobromus</i> | 3.38 | 0.50 | 0.00 | 0.04 |
| Actinopterygii | <i>Notropis photogenis</i> | 3.38 | 0.50 | 0.00 | 0.01 |
| Actinopterygii | <i>Notropis photogenis</i> | 3.38 | 0.50 | 0.00 | 0.01 |
| Actinopterygii | <i>Oncorhynchus tshawytscha</i> | 9 | 0.56 | 0.08 | 0.24 |
| Actinopterygii | <i>Oncorhynchus tshawytscha</i> | 9 | 0.56 | 0.08 | 0.24 |
| Actinopterygii | <i>Oncorhynchus tshawytscha</i> | 9 | 0.56 | 0.08 | 0.24 |
| Actinopterygii | <i>Opsopoeodus emiliae</i> | 4.4 | 0.51 | 0.01 | 0.09 |
| Actinopterygii | <i>Pimephales promelas</i> | 2 | 0.50 | 0.00 | 0.01 |
| Actinopterygii | <i>Zoarces viviparus</i> | 10 | 0.55 | 0.04 | 0.14 |
| Actinopterygii | <i>Zoarces viviparus</i> | 10 | 0.81 | 0.22 | 0.60 |
| Actinopterygii | <i>Zoarces viviparus</i> | 10 | 0.72 | 0.16 | 0.45 |
| Aves | <i>Anas laysanensis</i> | 12 | 3.17 | 2.80 | 0.99 |
| Aves | <i>Anas laysanensis</i> | 12 | 3.35 | 2.91 | 0.99 |
| Aves | <i>Anas laysanensis</i> | 12 | 2.89 | 2.60 | 0.99 |
| Aves | <i>Anser anser</i> | 31 | 5.01 | 4.12 | 0.99 |
| Aves | <i>Anser anser</i> | 31 | 6.54 | 5.71 | 0.99 |
| Aves | <i>Anser anser</i> | 31 | 3.94 | 3.06 | 0.99 |
| Aves | <i>Anthropoides paradiseus</i> | 27 | 4.54 | 4.14 | 0.96 |
| Aves | <i>Bonasa umbellus</i> | 11 | 1.15 | 0.46 | 0.92 |
| Aves | <i>Bonasa umbellus</i> | 11 | 0.90 | 0.27 | 0.77 |
| Aves | <i>Bonasa umbellus</i> | 11 | 1.08 | 0.39 | 0.99 |
| Aves | <i>Bonasa umbellus</i> | 11 | 1.25 | 0.54 | 0.94 |
| Aves | <i>Bonasa umbellus</i> | 11 | 1.69 | 0.93 | 0.97 |
| Aves | <i>Bonasa umbellus</i> | 11 | 1.21 | 0.51 | 0.91 |
| Aves | <i>Bonasa umbellus</i> | 11 | 1.04 | 0.37 | 0.94 |
| Aves | <i>Bonasa umbellus</i> | 11 | 1.05 | 0.38 | 0.88 |
| Aves | <i>Bostrychia hagedash</i> | 16 | 3.19 | 2.36 | 1.00 |
| Aves | <i>Buteo solitarius</i> | 17 | 1.88 | 1.31 | 0.82 |
| Aves | <i>Buteo solitarius</i> | 17 | 4.06 | 3.75 | 0.99 |
| Aves | <i>Buteo solitarius</i> | 17 | 2.67 | 2.28 | 0.93 |
| Aves | <i>Calidris temminckii</i> | 12.9 | 2.64 | 1.83 | 1.00 |
| Aves | <i>Calyptorhynchus lathamii</i> | 44.47 | 6.91 | 6.08 | 0.97 |

| | | | | | |
|----------|---|-------|-------|-------|------|
| Aves | <i>Campylorhynchus brunneicapillus</i> subsp. <i>sandiegensis</i> | 7.3 | 1.23 | 0.59 | 0.81 |
| Aves | <i>Centrocercus minimus</i> | 7 | 1.11 | 0.43 | 0.98 |
| Aves | <i>Centrocercus minimus</i> | 7 | 1.11 | 0.46 | 0.79 |
| Aves | <i>Certhia americana</i> | 8.2 | 1.03 | 0.43 | 0.97 |
| Aves | <i>Chen caerulescens</i> | 27.5 | 4.98 | 4.09 | 1.00 |
| Aves | <i>Falco naumanni</i> | 10.9 | 1.52 | 0.85 | 0.83 |
| Aves | <i>Falco peregrinus</i> subsp. <i>anatum</i> | 15.81 | 2.54 | 1.80 | 0.91 |
| Aves | <i>Fulmarus glacialis</i> | 51 | 11.06 | 10.15 | 1.00 |
| Aves | <i>Gavia immer</i> | 24.1 | 1.89 | 1.33 | 0.79 |
| Aves | <i>Gavia immer</i> | 24.1 | 1.85 | 1.29 | 0.79 |
| Aves | <i>Gavia immer</i> | 24.1 | 1.92 | 1.37 | 0.80 |
| Aves | <i>Gyps coprotheres</i> | 30.55 | 6.53 | 5.80 | 0.98 |
| Aves | <i>Haliaeetus albicilla</i> | 42 | 5.35 | 4.45 | 1.02 |
| Aves | <i>Haliaeetus albicilla</i> | 42 | 4.66 | 3.77 | 1.00 |
| Aves | <i>Lagopus leucura</i> | 15 | 0.94 | 0.31 | 0.74 |
| Aves | <i>Lagopus leucura</i> | 15 | 1.00 | 0.35 | 0.78 |
| Aves | <i>Lagopus muta</i> | 12 | 1.38 | 0.68 | 0.84 |
| Aves | <i>Lagopus muta</i> | 12 | 1.17 | 0.51 | 0.76 |
| Aves | <i>Lagopus muta</i> subsp. <i>japonica</i> | 12 | 2.25 | 1.42 | 1.17 |
| Aves | <i>Larus heermanni</i> | 29.87 | 5.24 | 4.44 | 1.05 |
| Aves | <i>Milvus migrans</i> | 24 | 2.38 | 1.63 | 0.91 |
| Aves | <i>Nipponia nippon</i> | 25.8 | 2.73 | 1.90 | 1.02 |
| Aves | <i>Pernis apivorus</i> | 29 | 5.00 | 4.10 | 1.01 |
| Aves | <i>Phalacrocorax auritus</i> | 22.5 | 2.06 | 1.37 | 0.82 |
| Aves | <i>Sterna hirundo</i> | 33 | 3.52 | 2.87 | 0.90 |
| Aves | <i>Sterna hirundo</i> | 33 | 2.58 | 1.92 | 0.85 |
| Aves | <i>Sternula antillarum</i> subsp. <i>browni</i> | 24 | 2.70 | 2.08 | 0.93 |
| Aves | <i>Strix occidentalis</i> subsp. <i>occidentalis</i> | 22.22 | 4.06 | 3.21 | 0.99 |
| Aves | <i>Thalassarche melanophris</i> | 43.7 | 2.32 | 1.57 | 0.76 |
| Aves | <i>Turdus torquatus</i> | 9.1 | 0.57 | 0.05 | 0.22 |
| Aves | <i>Turdus torquatus</i> | 9.1 | 0.61 | 0.07 | 0.28 |
| Aves | <i>Turdus torquatus</i> | 9.1 | 0.55 | 0.03 | 0.15 |
| Aves | <i>Vermivora chrysoptera</i> | 7.9 | 0.91 | 0.28 | 0.73 |
| Mammalia | <i>Alces alces</i> | 29.75 | 5.28 | 4.49 | 0.99 |
| Mammalia | <i>Alces alces</i> | 29.75 | 3.26 | 2.59 | 0.91 |
| Mammalia | <i>Alces alces</i> | 29.75 | 4.63 | 3.76 | 1.62 |
| Mammalia | <i>Alces alces</i> | 29.75 | 2.31 | 1.54 | 1.21 |
| Mammalia | <i>Brachyteles hypoxanthus</i> | 40 | 7.94 | 7.78 | 1.00 |
| Mammalia | <i>Callorhinus ursinus</i> | 21 | 4.30 | 3.52 | 1.00 |
| Mammalia | <i>Callospermophilus lateralis</i> | 10.4 | 1.00 | 0.40 | 0.83 |
| Mammalia | <i>Canis lupus</i> | 20.6 | 1.95 | 1.55 | 0.95 |
| Mammalia | <i>Capra ibex</i> | 20.71 | 11.77 | 10.89 | 1.10 |

| | | | | | |
|----------|---|-------|-------|-------|------|
| Mammalia | <i>Capra ibex</i> | 20.71 | 9.67 | 9.00 | 1.04 |
| Mammalia | <i>Capra ibex</i> | 20.71 | 11.61 | 10.65 | 1.37 |
| Mammalia | <i>Capra ibex</i> | 20.71 | 10.24 | 9.28 | 1.22 |
| Mammalia | <i>Cebus capucinus</i> | 54 | 12.76 | 12.16 | 0.99 |
| Mammalia | <i>Cervus elaphus</i> | 31.5 | 9.69 | 8.76 | 1.12 |
| Mammalia | <i>Cervus elaphus</i> | 31.5 | 1.51 | 0.89 | 0.79 |
| Mammalia | <i>Cervus elaphus</i> | 31.5 | 1.80 | 1.16 | 0.85 |
| Mammalia | <i>Cervus elaphus</i> | 31.5 | 3.31 | 2.56 | 0.99 |
| Mammalia | <i>Elephas maximus</i> | 65.5 | 28.40 | 27.68 | 1.01 |
| Mammalia | <i>Eumetopias jubatus</i> | 32.8 | 3.38 | 2.53 | 0.99 |
| Mammalia | <i>Eumetopias jubatus</i> | 32.8 | 5.40 | 4.57 | 0.96 |
| Mammalia | <i>Eumetopias jubatus</i> | 32.8 | 6.47 | 5.59 | 1.21 |
| Mammalia | <i>Eumetopias jubatus</i> | 32.8 | 3.32 | 2.48 | 1.44 |
| Mammalia | <i>Gorilla beringei</i> | 60.1 | 17.26 | 16.83 | 1.00 |
| Mammalia | <i>Gorilla beringei</i> | 60.1 | 15.15 | 14.70 | 1.00 |
| Mammalia | <i>Halichoerus grypus</i> | 42.9 | 8.28 | 7.53 | 0.98 |
| Mammalia | <i>Leptonychotes weddellii</i> | 48.13 | 4.67 | 3.87 | 0.92 |
| Mammalia | <i>Macaca mulatta</i> | 40 | 11.24 | 10.73 | 1.00 |
| Mammalia | <i>Macaca mulatta</i> | 40 | 11.46 | 10.84 | 1.00 |
| Mammalia | <i>Macaca mulatta</i> | 40 | 10.47 | 10.07 | 1.00 |
| Mammalia | <i>Macaca mulatta</i> | 40 | 11.27 | 10.63 | 1.00 |
| Mammalia | <i>Marmota flaviventris</i> | 21.2 | 1.64 | 0.92 | 0.91 |
| Mammalia | <i>Mirounga leonina</i> | 39 | 4.88 | 3.99 | 0.98 |
| Mammalia | <i>Mustela erminea</i> | 12.5 | 1.02 | 0.36 | 0.75 |
| Mammalia | <i>Odocoileus virginianus</i> | 23 | 2.13 | 1.49 | 0.78 |
| Mammalia | <i>Onychogalea fraenata</i> | 7.4 | 2.52 | 1.94 | 0.99 |
| Mammalia | <i>Orcinus orca</i> | 90 | 22.39 | 21.49 | 1.01 |
| Mammalia | <i>Orcinus orca</i> | 90 | 20.19 | 19.30 | 1.00 |
| Mammalia | <i>Orcinus orca</i> | 90 | 24.83 | 23.94 | 1.01 |
| Mammalia | <i>Ovis aries</i> | 22.8 | 4.00 | 3.25 | 0.95 |
| Mammalia | <i>Ovis canadensis</i> subsp. <i>sierrae</i> | 19.95 | 5.00 | 4.48 | 0.98 |
| Mammalia | <i>Ovis canadensis</i> subsp. <i>sierrae</i> | 19.95 | 5.01 | 4.49 | 0.98 |
| Mammalia | <i>Ovis canadensis</i> subsp. <i>sierrae</i> | 19.95 | 3.53 | 3.41 | 1.00 |
| Mammalia | <i>Ovis canadensis</i> subsp. <i>sierrae</i> | 19.95 | 3.96 | 3.24 | 0.96 |
| Mammalia | <i>Ovis canadensis</i> subsp. <i>sierrae</i> | 19.95 | 4.85 | 4.25 | 0.98 |
| Mammalia | <i>Ovis canadensis</i> subsp. <i>sierrae</i> | 19.95 | 3.51 | 2.77 | 0.95 |
| Mammalia | <i>Ovis canadensis</i> subsp. <i>sierrae</i> | 19.95 | 4.35 | 3.63 | 0.97 |
| Mammalia | <i>Ovis canadensis</i> | 19.95 | 5.57 | 4.80 | 1.01 |
| Mammalia | <i>Ovis canadensis</i> | 19.95 | 4.40 | 3.60 | 0.99 |
| Mammalia | <i>Ovis canadensis</i> | 19.95 | 4.97 | 4.18 | 1.00 |
| Mammalia | <i>Ovis canadensis</i> | 19.95 | 4.87 | 4.01 | 1.03 |
| Mammalia | <i>Pan troglodytes</i> subsp. <i>schweinfurthii</i> | 57.2 | 16.61 | 15.82 | 1.00 |
| Mammalia | <i>Panthera pardus</i> | 27.3 | 2.43 | 1.70 | 0.84 |

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|----------|--|-------|------|------|------|
| Mammalia | <i>Papio cynocephalus</i> | 37.5 | 9.41 | 8.83 | 0.99 |
| Mammalia | <i>Phoca vitulina</i> | 47.6 | 2.09 | 1.27 | 1.08 |
| Mammalia | <i>Phoca vitulina</i> | 47.6 | 2.29 | 1.46 | 1.37 |
| Mammalia | <i>Phocarcos hookeri</i> | 26 | 5.64 | 4.75 | 1.06 |
| Mammalia | <i>Presbytis thomasi</i> | 20 | 4.07 | 3.29 | 0.97 |
| Mammalia | <i>Propithecus edwardsi</i> | 24 | 4.08 | 3.51 | 0.94 |
| Mammalia | <i>Propithecus verreauxi</i> | 31 | 9.11 | 8.46 | 1.00 |
| Mammalia | <i>Rangifer tarandus</i> | 21.8 | 2.91 | 2.35 | 0.94 |
| Mammalia | <i>Rangifer tarandus</i> | 21.8 | 3.88 | 3.37 | 0.98 |
| Mammalia | <i>Rangifer tarandus</i> subsp. <i>platyrhynchus</i> | 21.8 | 7.98 | 7.40 | 1.02 |
| Mammalia | <i>Sousa chinensis</i> | 50.39 | 9.71 | 8.79 | 1.21 |
| Mammalia | <i>Sousa chinensis</i> | 50.39 | 9.67 | 8.75 | 1.21 |
| Mammalia | <i>Tamiasciurus hudsonicus</i> | 9.8 | 1.32 | 0.65 | 1.02 |
| Mammalia | <i>Urocitellus armatus</i> | 9 | 1.09 | 0.41 | 0.92 |
| Mammalia | <i>Urocitellus beldingi</i> | 9 | 3.25 | 2.53 | 1.11 |
| Mammalia | <i>Ursus americanus</i> | 34 | 3.53 | 2.81 | 0.92 |
| Mammalia | <i>Ursus americanus</i> | 34 | 3.37 | 2.54 | 0.92 |
| Mammalia | <i>Ursus arctos</i> subsp. <i>horribilis</i> | 39.25 | 4.62 | 3.71 | 1.01 |
| Mammalia | <i>Zalophus californianus</i> | 35.7 | 5.34 | 4.49 | 1.02 |
| Mammalia | <i>Zalophus californianus</i> | 35.7 | 4.12 | 3.28 | 1.09 |
| Reptilia | <i>Chrysemys picta</i> | 61 | 3.13 | 2.28 | 2.38 |
| Reptilia | <i>Chrysemys picta</i> | 61 | 1.43 | 0.79 | 0.64 |
| Reptilia | <i>Crocodylus johnsoni</i> | 47.34 | 1.79 | 1.16 | 0.75 |
| Reptilia | <i>Crocodylus johnsoni</i> | 47.34 | 2.48 | 1.83 | 0.83 |
| Reptilia | <i>Crocodylus johnsoni</i> | 47.34 | 1.35 | 0.76 | 0.66 |
| Reptilia | <i>Cryptophis nigrescens</i> | 21 | 1.67 | 0.98 | 0.81 |
| Reptilia | <i>Hoplocephalus bungaroides</i> | 31 | 2.64 | 1.85 | 0.88 |
| Reptilia | <i>Kinosternon subrubrum</i> | 40 | 1.62 | 0.96 | 0.72 |
| Reptilia | <i>Kinosternon subrubrum</i> | 40 | 0.80 | 0.21 | 0.36 |
| Reptilia | <i>Kinosternon subrubrum</i> | 40 | 3.15 | 2.42 | 0.89 |

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