The significance of postreproductive lifespans in killer whales: a comment on Robeck et al.

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Robeck et al. (2015) claim that reproductive and actuarial senescence is common in mammalian species and therefore not an unexpected finding in killer whales. However, in most mammals, reproductive and somatic senescence are aligned, and reproduction gradually declines with age. In contrast, there is a substantial evidence that reproductive senescence is unusually accelerated relative to somatic senescence in resident killer whales, resulting in a prolonged postreproductive lifespan. We demonstrate that a postreproductive lifespan is a key component of resident killer whale life history, and is robust to reasonable error in age estimates.

Key words: killer whale, life history, menopause, postreproductive lifespan

Robeck et al. claim that reproductive and actuarial senescence "is common in mammalian species… and it therefore should not be considered an unexpected finding in killer whales" (p. 13).

We agree with the statement that reproductive senescence and actuarial senescence (which we will refer to as "somatic senescence") are both widespread in mammalian species (Nussey et al. 2013). Indeed, both reproductive and somatic senescence are for many organisms inescapable facts of life (Promislow 1991; Kirkwood and Austad 2000). In natural populations of most species, a large proportion of individuals do not die of old age, but from extrinsic factors such as predation, starvation, or disease. This reduces the proportion of older individuals in the population (Medawar 1952; Hamilton 1966). Alleles that confer advantages early in life by increasing early life fecundity can spread to fixation even if they have deleterious effects in later life (Williams 1957; Charlesworth 1994). This declining strength of selection with age has led to the evolution of physiological mechanisms leading to both reproductive and somatic senescence (Kirkwood 1977; Gavrilov and Gavrilova 2001).

The key point missed by Robeck et al. is that while reproductive and somatic senescence are widespread, in the vast majority of species, they are aligned and reproduction gradually declines with age (Jones et al. 2014). In contrast, there is substantial evidence that they are not aligned in female humans, resident killer whales (*Orcinus orca*), and short-finned pilot whales (*Globicephala macrorhynchus*), with reproductive senescence accelerated relative to somatic senescence (Marsh and Kasuya 1984, 1986; Olesiuk et al. 1990). The result is a prolonged postreproductive lifespan of females who are otherwise healthy (Croft et al. 2015). Thus, killer whales are not unusual because they exhibit reproductive senescence, but because their rate of reproductive senescence is highly accelerated relative to somatic senescence, leading to an extraordinarily long postreproductive life. This postreproductive lifespan can be explained in evolutionary terms because a high proportion of females (relative to natural populations of most species) live to old age, thus increasing selection on late-life effects (Foote 2008), and because old females can confer significant survival or reproductive benefits to their kin (Foster et al. 2012). If the old female herself reproduces, it may reduce these benefits,

perhaps because of increased mortality risk (and thus the cessation of the benefits), lesser ability to assist, or competition from new offspring.

The evidence for postreproductive lifespan in wild populations of killer whales comes from long-term individual-based studies on 2 populations of resident killer whales in the North Pacific consisting of over 40 years of individual demographic and social data for more than 600 individuals (Olesiuk et al. 1990; Towers et al. 2015). This long-term study started in 1974 and at this point the ages of individuals already living were estimated according to previously described methods (Bigg et al. 1990). Briefly, birth dates for juveniles born before the start of the study were estimated by subtracting the estimated age of maturity (15 years for both sexes) from the year they matured. Dates of birth for adult females born before the start of the study were estimated by subtracting 15 years from the estimated year of birth of her oldest offspring, which was assumed to be her 1st viable calf. Dates of birth of adult males born before the start of the study were estimated by assuming that they attained physical maturity the year they were 1st observed.

Robeck et al. argue that ages are overestimated leading to an overrepresentation of old individuals in the population. Their argument is based on their calculated probability of whales reaching old age, using estimated age-specific survival data from Southern Alaskan resident killer whales (Matkin et al. 2013). Based on their calculated survival probabilities, they propose a maximum longevity between 60 and 70 years for females. This is based on their calculated probabilities of female survival to 60, 70, and 80 of 1 in 37, 1 in 431, and 1 in 4,980, respectively. Robeck et al. then extrapolate their calculations to comment on the expected ages of the North Pacific resident killer whales.

Comparing life history across populations is interesting but extrapolating between populations can be problematic, and it is also useful to look at the probabilities of female survival directly for many populations. When we calculate this directly from life tables based the estimated ages in the combined Northern and Southern resident populations in the North Pacific, we find probabilities (rounded to the nearest whole number) of female survival to 60, 70, and 80 of 1 in 4, 1 in 6, and 1 in 9, respectively (with the survival probability being > 0.93 for each age class in the life table). For the Southern Residents alone, these probabilities are 1 in 4, 1 in 6, and 1 in 9, and for the Northern Residents they are 1 in 4, 1 in 7, and 1 in 12. These calculations are in stark contrast with those reported by Robeck et al., yet are based on the same logic using probabilities calculated from estimated ages. Note that even when we follow the suggestion of Robeck et al. and constrain the maximum estimated age of a whale to 70 then the probability of a female in the combined Northern and Southern resident populations reaching 70, based on age-specific survival, remains 1 in 6, which is substantially higher than the 1 in 431 suggested by Robeck et al. Overall this suggests that there are either differences in the life histories of the Alaskan population compared to the Northern and Southern resident populations or that differences in age estimates have come about due to the differences in the length of observation of these populations (40 years for the Southern/Northern residents, and 20 years plus 5 partial years for the Alaskan residents) and that future work is needed to unravel this. It is important to note that resident killer whales are one of a number of killer whale ecotypes that differ in their prey specializations and social structure (Baird and Whitehead 2000; Riesch et al. 2012). Changes to life history traits can evolve rapidly (15 generations) and vary intraspecifically in response to changes in the level of age-dependent extrinsic mortality (Reznick 1997). Although the Alaskan and Southern/Northern Resident killer whales are believed to be the same ecotype, they do not interbreed and it is therefore possible that they have evolved different life histories. We should therefore be cautious in generalizing across killer whale populations.

It is also important to recognize that most females in the Northern/Southern Resident communities cease reproduction in their late 30s to early 40s and hence that a substantial proportion of wild females typically live beyond their reproductive years (Olesiuk et al. 2005). To demonstrate the significance of the postreproductive lifespan in the Northern and Southern resident killer whales, we quantify it with a measure of postreproductive lifespan—postreproductive representation (PrR; the proportion of adult years lived which are postreproductive)—recently developed by Levitis and Bingaman (2011). First, we calculate the PrR value based on current age estimates for the Northern and Southern resident killer whale populations and compare this value to published PrR values for other species. Second, we show that this measure is robust to the errors in age estimates of these wild whales as proposed by Robeck et al. Whales that were not observed as calves, but later aged at the start of the study, were excluded from analyses up to and including the 1st year of sighting to avoid a positive bias in survival to that age. To avoid overestimating early life survival, we included individuals of unknown sex (all ≤ 15 years old, thus affecting those individuals who become reproductive before 15) in the calculation but randomized the sex of these individuals ($n = 1,000$ permutations) to calculate mean survival for those age classes. The PrR for the resident killer whales based on current age estimates is 0.282 (Table 1). Comparison to other values in Table 1 highlights that a high PrR is uncommon among animals in the wild and indeed that resident killer whales, short-finned pilot whales, and humans stand out among mammals for having high and significant PrR values. In contrast, the values of PrR in wild populations of other mammals in the table are all less than 0.06.

To determine the effect of age estimates on the significance of the postreproductive lifespan, we pushed forward the estimated dates of birth of the Northern and Southern resident populations so that any individual with an estimated age over X years was truncated (i.e., a maximum age of X) for $X = \{80,70,60,50\}$. Where necessary we iteratively pushed forward the date of birth of other whales until the condition was met that their mother was at least 10 years old at their birth. Even with these amendments, we find a significant and prolonged postreproductive lifespan at all maximum ages (Table 1). This analysis clearly demonstrates that the postreproductive lifespan in resident killer whales is a substantial and significant life history

Table 1.—Published values of female postreproductive representations (PrRs). Also shown are PrRs for the resident killer whales (*Orcinus orca*) calculated using published data (Foster et al. 2012). The table is adapted from Croft et al. (2015).

Species	Population	PrR	Reference
Homo sapiens	!Kung	0.425	Levitis et al. (2013)
Homo sapiens	Ache	0.439	Levitis et al. (2013)
Homo sapiens	Haiti 2002	0.460	Levitis et al. (2013)
Homo sapiens	Sweden 1751	0.477	Levitis et al. (2013)
Homo sapiens	Hadza	0.481	Levitis et al. (2013)
Blue monkey (*Cercopithecus mitis*)	Wild	0.02	Alberts et al. (2013)
Blue monkey (*Cercopithecus mitis*)	Wild	0.041	Levitis et al. (2013)
Chimpanzee (*Pan troglodytes*)	Wild	0.018	Levitis et al. (2013)
Chimpanzee (*Pan troglodytes*)	Wild	0.02	Alberts et al. (2013)
Gorilla (*Gorilla beringei*)	Wild	0.04	Alberts et al. (2013)
Hamadryas baboon (*Papio hamadryas*)	Wild	0.005	Levitis et al. (2013)
Muriquis (*Brachyteles hypoxanthus*)	Wild	0.06	Alberts et al. (2013)
Rhesus macaque (*Macaca mulatta*)	Wild	0.007	Levitis et al. (2013)
Sifaka (*Propithecus verreauxi*)	Wild	0.02	Alberts et al. (2013)
White-faced capuchin (*Cebus capucinus*)	Wild	0.04	Alberts et al. (2013)
Yellow baboon (*Papio cynocephalus*)	Wild	0.01	Alberts et al. (2013)
Short-finned pilot whale (*Globicephala macrorhynchus*)	Wild	0.28	Levitis and Bingaman (2011)
Resident killer whales (*Orcinus orca*; *based on current age estimates*)	Wild	0.282, $P = 0.001$	
[based on maximum age of 80 years for females]		0.269, $P = 0.001$	
[based on maximum age of 70 years for females]		0.244, $P = 0.001$	
[based on maximum age of 60 years for females]		0.222, $P = 0.001$	
[based on maximum age of 50 years for females]		0.157, $P = 0.036$	

stage and not simply an artifact due to age estimation errors as proposed by Robeck et al.

Robeck et al. state that reproductive senescence in killer whales is "often erroneously termed menopause…" We focus here not on debating this definition but on the evidence that reproductive senescence is decoupled from somatic senescence in resident killer whale populations. However, as with many terms, the use of menopause has changed over time. The term menopause first appeared in the early 19th century medical literature to describe the cessation of menstruation (De Gardanne 1821). A strict modern medical definition of menopause refers to the permanent cessation of menstruation resulting from loss of ovarian follicular activity (World Health Organization Scientific Group 1981). Arguments against using the term in reference to whales are based on the fact that whales do not menstruate. However, the usage of the term menopause is broader in the scientific literature. For example, the term "male menopause" has been used to refer to the physiological and emotional changes that tend to occur in males during midlife. The use of the term menopause has also had a wider application to nonhuman animals (Cohen 2004; Uematsu et al. 2010; Brent et al. 2015). For example, Cohen (2004) used the term menopause to describe the "irreversible loss of the physiological capacity to produce offspring due to intrinsic biological factors." Importantly, it allows for a distinction to be made between reproductive termination in late life where females maintain reproductive capacity (e.g., reproductive termination is socially enforced—Hogendoorn and Leys 1993; Richardson et al. 2007) and where the termination of reproduction is due to physiological changes that are irreversible (e.g., Uematsu et al. 2010). Postreproductive lifespan is a continuum (which can be measured with PrR) but there are a few standout cases where a substantial postreproductive lifespan is due to physiological changes that are irreversible and these species have been loosely termed as exhibiting menopause. For example, there is direct evidence for cessation of ovulation in postreproductive female short-finned pilot whales (Kasuya and Marsh 1984). Such a widening of the usage of the term menopause has great utility in studies on nonhuman animals. We endorse this wider use of the term menopause and advocate that it allows for important biological distinction to be made between the mechanisms that drive postreproductive lifespans in nonhuman animals.

In conclusion, we demonstrate that a postreproductive lifespan is a key component of the life history of resident killer whales. The significance of this life history trait is independent of potential error in the age estimates of older whales in the population. It may take up to another 60 years of direct observations before we have directly observed an individual from birth to the maximum age at death. Only then will we be able to establish the exact longevity of these whales in the wild. In the meantime, however, the evidence that resident killer whales exhibit a postreproductive lifespan approaching that of humans is overwhelming and as such these populations provide a rare opportunity to test the current theoretical framework for the evolution of prolonged life after reproduction (Foote 2008; Johnstone and Cant 2010; Foster et al. 2012; Brent et al. 2015).

ACKNOWLEDGMENTS

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