Adaptive Prolonged Postreproductive Life Span in Killer Whales

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The evolution of a prolonged postreproductive life span has attracted considerable interdisciplinary attention, primarily because of the long postmenopausal life span seen in humans (1). Two mechanisms have been proposed to underpin prolonged postreproductive life span: (i) an epiphenomenon of increased longevity, in which evolutionary benefits accrue only during the reproductive phase with no additional fitness benefits after the last reproductive event, and (ii) an evolved adaptation in which postreproductive life span increases the survival of an individual's genes, increasing its inclusive fitness. There is mounting evidence that postreproductive human females increase the reproductive success and survival of their offspring (2, 3). Although helping in some postreproductive female cetaceans (4) suggests an adaptive benefit, there has been no evidence that a similar phenomenon occurs in nonhuman animals.

With multigenerational demographic records based on photographic censuses (1974 to 2010) of the Southern and Northern resident killer whale (*Orcinus orca*) populations in coastal waters off Washington state, USA, and British Columbia, Canada [see (5) for details], we used a Cox proportional hazards model (6) to examine the consequences of a mother's death on offspring survival.

This unique data set consisted of 589 individually identifiable animals, of which 297 died during the study period (6).

Resident killer whales have the longest postreproductive life span of all nonhuman animals: Females stop reproducing in their 30s to 40s but can survive into their 90s (5). Because neither sex disperses from the maternal group (7), theory based on kinship dynamics (4) predicts that female's relatedness to her group increases with age and that old mothers maximize their fitness by ensuring their offspring's survival and reproductive success. There is an asymmetry, however, in the benefits of helping sons and daughters. Mating occurs outside of the matriline; thus, a son's offspring are raised by another group (where any rearing costs are incurred), whereas a daughter's offspring are raised within the group, increasing within-group competition (4). Old mothers can therefore maximize inclusive fitness benefits by directing care toward sons (4).

Postreproductive mothers are known to have little effect on their daughter's reproductive success in resident killer whales (8). However, we show that both postreproductive and reproductive females increase their own offspring's survival, particularly older male offspring (Fig. 1 and table S1). For male offspring ≤30 years old, there is a 3.1-fold increase in mortality risk in the year after their mother's death (Fig. 1). For males >30, this risk increases to 8.3-fold (Fig. 1). In contrast, female offspring ≤30 show no increase in mortality risk, whereas those >30 show some increase in risk (2.7-fold) in the year after their mother's death (Fig. 1). Importantly, the magnitude of this effect does not differ between reproductive and postreproductive females (6). Indeed, for offspring >30, the death of a postreproductive mother increases mortality risk 13.9-fold in sons and 5.4-fold in daughters in the year after their mother's death.

Our results demonstrate an adaptive benefit to a prolonged postreproductive life span in killer whales. Because reproductive success increases with age in male killer whales (9), increasing the survival of older male offspring will maximize inclusive fitness (4). Resident killer whales are unusual in that mothers maintain strong social relations with their adult sons throughout their lives (7). Mothers may increase the survival of their adult sons in a number of ways, including assisting in foraging and providing support during agonistic encounters (10). Crucially, the fact that mothers increase the survival of male offspring, which do not terminate reproduction early (9), may explain why killer whales have evolved the longest postreproductive life span of any nonhuman animal.

References and Notes

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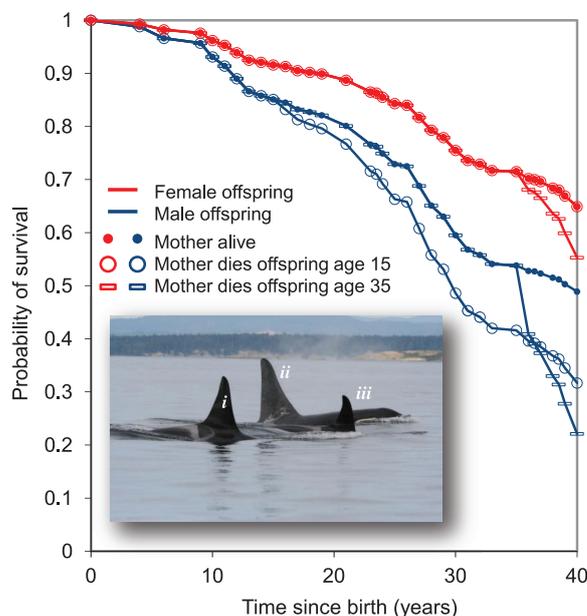*To whom correspondence should be addressed. E-mail: d.p.croft@exeter.ac.uk

Fig. 1. Survival curves derived from a Cox proportional hazards model (6) for male and female offspring experiencing their mother's death at different ages. (**Inset**) Adult sons (i and ii) traveling with their postreproductive mother (iii).

Legend:
- Female offspring
- Male offspring
- Mother alive
- Mother dies offspring age 15
- Mother dies offspring age 35

Y-axis: Probability of survival
X-axis: Time since birth (years)