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# Costly sons do not lead to adaptive sex ratio adjustment in pilot whales, *Globicephala melas*

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Maternal investment in reproduction and parental care is an important determinant of both offspring and maternal fitness. However, optimal investment strategies may differ depending on offspring sex, potentially resulting in a sex-biased distribution of maternal resources or adaptive variation in offspring sex ratio. We used morphometric and genetic data collected from over 3400 long-finned pilot whales in 40 pods to investigate whether females experience differential costs of producing sons and daughters and whether they differentially invest in male and female offspring. We found that male calves grew faster than female calves during the first 5 years of life, suggesting that sons may require greater investment from lactating mothers. This appeared to result in mothers experiencing a higher cost to future reproductive opportunities when producing male offspring as the presence of dependent sons (but not daughters) reduced the probability that a female would be pregnant. Despite these costs, we found no evidence that mothers adaptively adjusted their investment in sons and daughters according to their body condition or their social and physical environment. These results suggest that mothers may be constrained from biasing investment in the sexes, or that additional benefits may be masking such costs.

Maternal investment includes the resources, energy and time used for reproduction. While investment in offspring contributes to maternal fitness through increasing offspring survival, large investments can impose costs on maternal health, survival and longevity (Lester, Shuter, & Abrams, 2004). Consequently, females are likely to be under selection to adjust their investment in offspring adaptively according to the resources available to them (Clutton-Brock, Albon, & Guinness, 1981).

In cases where the reproductive value of male and female offspring is influenced differently by variation in maternal investment, mothers may be selected to bias resource allocation towards offspring of one sex (Charnov, 1982). In polygynous species, females are usually a limiting resource over which males should compete for access, with males in good condition outcompeting smaller, poorer quality males for access to reproductive females. Such species often show sexual dimorphism, with males growing faster or for longer than females, and hence attaining a larger adult size (Clutton-Brock, 2007). Accordingly, male offspring may require greater energetic investment from their mothers during gestation and/or lactation. Such differences have been shown in many studies; for example, males often weigh more at birth or receive more milk (Duncan, Harvey, & Wells, 1984; Ono & Boness, 1996) or richer milk (Hinde, 2009; Robert & Braun, 2012).

In polygynous species, differential maternal investment often results in differential fitness costs to the mother. For example, red deer hinds, *Cervus elaphus*, and bighorn ewes, *Ovis canadensis*, that give birth to a son are less likely to reproduce successfully in the following breeding season than those that give birth to a daughter (Bérubé, Festa-Bianchet, & Jorgenson, 1996; Clutton-Brock et al., 1981) and female African elephants, *Loxodonta africana*, have greater interbirth intervals after weaning sons (Lee & Moss, 1986). Similarly, female bank voles, *Myodes glareolus*, raising experimentally manipulated male-biased litters had higher energy requirements and produced smaller female offspring in their subsequent litters (Rutkowska, Koskela, Mappes, & Speakman, 2011). However, some studies have failed to find such effects. For example, studies of two highly polygynous and sexually dimorphic pinnipeds, the Antarctic fur seal, *Arctocephalus gazella* (Lunn & Arnould, 1997) and the northern elephant seal, *Mirounga angustirostris* (Kretzmann, Costa, & Le Boeuf, 1993) failed to find sex differences in various measures of maternal investment such as

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suckling rate, pup growth rate or size at weaning. Instead, male seals may invest more in growth postweaning in order to attain a larger adult size (Lunn & Arnould, 1997).

In addition to adjusting the quality of offspring produced, mothers can also adjust investment in the sexes by producing unequal numbers of male and female offspring. Trivers and Willard (1973) proposed that, in species in which maternal condition affects the fitness of male and female offspring differently, mothers in good condition should bias their offspring sex ratio in favour of the sex for which condition has the strongest impact on fitness. In polygynous species, mothers in good condition are expected to invest in sons while mothers in poor condition should invest in daughters, for which condition has less impact on fecundity. This model has been applied to a variety of mammalian species including ungulates (Sheldon & West, 2004), marsupials (Robert & Schwanz, 2011) and primates (Brown, 2001). In many cases, observations met the predictions, although studies of other species and even of the same species but at different population densities (Kruuk, Clutton-Brock, Albon, Pemberton, & Guinness, 1999) have failed to show a response (MacLeod & Clutton-Brock, 2013). This apparent variability has led some to question whether there is a common pattern, with suggestions of publication bias and the possibility that additional factors could affect the relationship between maternal condition and sex ratio (Brown & Silk, 2002; Sheldon & West, 2004).

In social species, sex differences in dispersal and cooperation may also affect the costs and benefits of investing in male and female offspring (Emlen, Emlen, & Levin, 1986; Hamilton, 1967). For example, sex differences in helping behaviour often occur in species that show cooperative care, where mothers with few helpers may benefit from overproducing the more helpful sex (Emlen et al., 1986; West & Sheldon, 2002). However, the benefits of producing philopatric helpers may be counteracted to some extent by local competition for food or mates, leading to the prediction that mothers should invest more in the dispersing (less helpful) sex when in poor condition, or when breeding on poor-quality territories (Wild & West, 2007). Here, the benefits of producing extra helpers may be outweighed by the costs of producing more competitors, leading to a density-dependent trade-off between costs and benefits of investment in a particular sex (Emlen et al., 1986). For example, Seychelles warblers, *Acrocephalus sechellensis*, show extreme adaptive modification of offspring sex ratio according to an interaction between resource availability and local competition on the natal territory, overproducing female helpers when on territories of sufficient quality to support additional group members (Komdeur, Daan, Tinbergen, & Mateman, 1997). As a consequence, the potential effects of sex differences in cooperation and competition should be taken into account when investigating maternal investment in the sexes.

Cetaceans offer an interesting system in which to study maternal investment. The generally larger, nonsocial baleen whales show reversed sexual dimorphism with females often attaining larger sizes than males (Clapham, 1996). In contrast, many Odontocetes (toothed whales, including dolphins) are highly social, living in groups of up to several hundred individuals or even more (Connor, Mann, Tyack, & Whitehead, 1998). Among Odontocetes, males are often larger than females and social interactions may be complicated and enduring. Thus, killer whales, *Orcinus orca*, live in small matrifocal groups known as pods, with sons staying with their mothers for their entire lives but mating with females in different pods (Foster et al., 2012). Similar systems appear to operate in closely related pilot whales, although with much larger pod sizes; social ties appear to be unusually strong, with extended maternal dependence and evidence of postweaning suckling (Amos, Schlötterer, & Tautz, 1993).

In this study, we explored factors influencing maternal investment and sex ratio biases in the long-finned pilot whale, which is a medium-sized whale that lives in groups of between 10 and 1000 animals (Ottensmeyer & Whitehead, 2003). Like its relative, the killer whale (Parsons, Balcomb, Ford, & Durban, 2009; Yurk, Barrett-Lennard, Ford, & Matkin, 2002), groups appear to be extremely long-lived, with individuals of both sexes apparently remaining in their natal pods all their lives (Amos, Barrett, & Dover, 1991; Amos et al., 1993). As male pod members can generally be excluded as fathers of offspring in their own pod using genetic methods, it has been hypothesized that mating is likely to occur between different pods when they meet or during male prospecting trips (Amos et al., 1991). Female pilot whales may live as long as 60 years, perhaps a third again as long as males, which live to a maximum age of around 45 years (Bloch, Desportes, Mouritsen, Skaaning, & Stefansson, 1993). Sexual size dimorphism has been observed in the long-finned pilot whale, with adult males reaching 625 cm in length, and adult females reaching 512 cm (Bloch, Lockyer, & Zachariassen, 1993). Pods generally have a female-biased sex ratio (Bloch, Desportes, et al., 1993), but the extent to which this is due to sex differences in survival, dispersal or sex ratio at birth is currently unclear.

We tested the prediction that juvenile male pilot whales will grow faster than female offspring during the period of maternal care, and hence will be likely to require greater investment from lactating mothers. We then investigated whether this in turn leads to mothers experiencing a higher cost to future reproductive opportunities of producing male offspring. Finally, we tested whether mothers adaptively adjust their investment in sons and daughters according to their body condition and their social and physical environment.

## METHODS

### Sample Collection

Data were obtained from a pilot whale drive fishery in the Faroe Islands (Zachariassen, 1993), where until recently pilot whales constituted a vital part of the local diet. Between 1986 and 1989, data were collected from 3470 animals from 40 pods as part of a Faroese government-funded research project on the biology of the pilot whale (Bloch, Desportes, et al., 1993). The sex and total body length of captured whales were recorded, and age was determined by counting the growth layer groups visible in a tooth section (Lockyer, 1993). There is substantial variation in the age at maturation, with some females reaching sexual maturity at 5 or 6 years old (mean 8.4 years, Bloch, Lockyer, et al., 1993), while other individuals (particularly males) do not reach maturity until 11–12 years old (Desportes, Saboureau, & Lacroix, 1993). For the purposes of this study, whales were split into two age classes. Individuals were classed as calves if they were 5 years old or younger, as offspring have been observed to suckle until this age (Desportes & Mouritsen, 1988). As females may give birth at age 6 years, individuals aged 6+ were considered to be adults and were included as potential mothers in maternity analyses. Owing to the extreme cohesion of pilot whale pods, it is believed that pods were sampled in their entirety (Amos et al., 1993); hence the size and sex ratio of each pod could be calculated. Only individuals classed as adults were included in the calculations of pod size and sex ratio. Reproductive status was allocated to females via a post mortem, which assessed the presence, length and the morphological sex of any fetus present. Owing to time constraints when sampling a large number of whales, it was not possible to take every measurement for each individual; hence gaps in the data occurred. Analyses