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Size-assortative pairing and discrimination of potential mates by humpback whales in the Hawaiian breeding grounds

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Assortative pairing, and its relation to mate choice, has rarely been documented in mammals. Using data collected during 1998–2007, we investigated size-assortative pairing as it relates to discrimination amongst potential mates in humpback whale, *Megaptera novaeangliae*, dyads in the Hawaiian breeding grounds. Across 67 male–female dyads in which both individuals were measured using underwater videogrammetry, male length was positively correlated with female length. Detailed analyses on the assessment of maturity by comparisons with whaling data revealed that mature-sized females associated almost exclusively with mature-sized males and had a significant preference for large mature-sized males. In contrast, mature-sized males were less discriminating in their associations with females and showed no significant preference for mature-sized females. However, mature-sized males that associated with immature-sized females were significantly smaller than males that associated with mature-sized females. Finally, immature-sized males tended to associate with immature-sized females. The sex differences in size preference by mature whales probably reflect the relatively high costs of mature females mating with small or immature males compared to the lower costs of mature males mating with small or immature females. Body size appears to influence the adoption of alternative mating tactics by males such that smaller mature males avoid the costs of competing for the highest-quality females and instead focus their attentions on smaller females that may or may not be mature. Overall, our results provide the first quantitative evidence of size-assortative pairing and female discrimination amongst potential mates in humpback whales and indeed in any cetacean species.

Over the past 20 years, a growing number of studies have examined assortative pairing (i.e. the association of a male and a female that possess at least one similar specific phenotypic trait) in sexually reproducing species (Crespi 1989; Harari et al. 1999; Shine et al. 2001; Preston et al. 2005; Hoefler 2007; Farrell et al. 2011). This effort has been fuelled largely by a fundamental long-term interest in mate choice and its consequences (Andersson 1994). For example, assortative mating (i.e. assortative pairing that results in mating) may have a profound influence on sexual selection, including genetic variation in traits associated with male reproductive success (Crespi 1989; Farrell et al. 2011). In many sexually reproducing species, body size has an important influence on male–female associations (Andersson 1994; Basolo 2004; Preston et al. 2005). Assortative mating based on body size has been found in a variety of taxa, including beetles (Brown 1993; Bernstein & Bernstein 1998; Harari et al. 1999), spiders (Hoefler 2007), toads (Boell & Linsenmair 1998), flies (Otronen 1993), shrimp (Santos-Filho & Pisaneschi 1997), snakes (Weatherhead et al. 2002), fish (McKaye 1986; van Oppen et al. 1998) and birds (Jawor et al. 2003; Komdeur et al. 2005; Christensen & Kleindorfer 2007). Although Crespi (1989) asserted that size-assortative mating is fairly ubiquitous in natural populations, few studies have investigated size-assortative mating in mammals (Preston et al. 2005).

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To our knowledge, neither assortative mating nor assortative pairing has been investigated quantitatively in cetaceans (reviewed in: Whitehead & Mann 2000; Mesnick & Ralls 2009). Here, we investigate size-assortative pairing in humpback whale, *Megaptera novaeangliae*, male–female dyads and its implications for mate choice.

Humpback whales migrate seasonally between high-latitude areas where they feed during summer and autumn months and low-latitude areas where they calve and breed during winter and spring months (Chittleborough 1965; Dawbin 1966; Baker et al. 1986; Katona & Beard 1990; cf. Mikhalev 1997). Mature and immature humpbacks of both sexes assemble on the breeding grounds (Nishiwaki 1959; Dawbin 1966; Craig et al. 2003). The mean age of sexual maturity in male and female humpbacks has been reported historically as approximately 5 years (Chittleborough 1965; Clapham 1992). However, recent studies and reassessments of the rate of accumulation of ear plug laminations suggest that mean age at sexual maturity may be 9–11 years (Gabriele et al. 2007; Best 2011). While on the breeding grounds, humpback whales, with the exception of calves, fast and rely on metabolized fat reserves for energy. Because large body size allows for greater accumulation of body fat (Calder 1984; Fedak et al. 2002), large body size may be favoured in humpback whales.

The mating system of humpback whales is poorly understood (Herman & Tavolga 1980; Clapham 1996, 2000; Craig et al. 2002; Cerchio et al. 2005; Smith et al. 2008). Females both with and without a calf are commonly observed in association with one or more male ‘escorts’ (Herman & Antinoja 1977; Craig et al. 2002). Copulation has never been observed in humpbacks (Pack et al. 2002; Herman et al. 2008), but escorts are assumed to be either seeking mating opportunities or engaging in postcopulatory mate guarding (Clapham 1996). When two or more escorts accompany a female, they often compete for proximity to the female through physical displays and aggression in what has been termed a ‘competitive group’ (Tyack & Whitehead 1983; Baker & Herman 1984; Clapham et al. 1992; Herman et al. 2008). Within a competitive group, the male defending the position closest to the female (‘nuclear animal’) is termed the ‘principal escort’; a male actively seeking to displace the principal escort is termed the ‘challenger’; and other males are termed ‘secondary escorts’ (Tyack & Whitehead 1983).

Male–male competition between humpbacks would be predicted on theoretical grounds because of pronounced sex differences in the parental investment of males and females (Trivers 1972). Males do not make any parental investment beyond fertilization, whereas females give birth to a single calf after a gestation period of just under 12 months, and calves are weaned after 10–12 months (Chittleborough 1958; Clapham & Mayo 1987; Baraff & Weinrich 1993). Although some females produce calves in consecutive years (e.g. Glockner-Ferrari & Ferrari 1990; Herman et al. 2011), most females do not experience postpartum ovulation with conception (Chittleborough 1965). Females give birth to a calf every 2–3 years on average (Baker et al. 1987; Barlow & Clapham 1997). This effectively removes a large proportion of females from the annual reproductive pool, resulting in an operational sex ratio on the breeding grounds that is heavily biased towards males (Herman & Tavolga 1980; Herman et al. 2011).

The substantial parental investment of female humpbacks suggests that they should be discriminating in their choice of mate. In many species where female parental investment is higher than that of males, females derive substantial fitness benefits from discriminating amongst males of differing quality and often show an active preference for large males over small males (Andersson 1994). However, female mating tactics and the factors influencing female mate choice have not been studied quantitatively in humpback whales, or in any other cetacean (Clapham 1996, 2000; Whitehead & Mann 2000; Mesnick & Ralls 2009). Some behavioural evidence suggests that female North Atlantic right whales, *Eubalaena glacialis*, may reject sexual advances by turning ventral side up, although active selection of particular males has not been demonstrated (Kraus & Hatch 2001). This particular behaviour has not been reported in female humpback whales, but Clapham’s (1992) report of a female humpback in a competitive group being aggressive towards a known subadult male was interpreted as a form of rejection. Herman et al. (2008) suggested that certain female humpback behaviours, such as extending a pectoral fin towards the principal escort and active maintenance of close proximity to it, could be interpreted as physical solicitation. Also, Clapham (2000) speculated that females facilitate the formation of competitive groups by slapping their body parts on the water’s surface.

Despite uncertainty surrounding the specific tactics that culminate in humpback whale mating, a few studies have investigated some of the factors likely to influence male mate choice in humpbacks. Craig et al. (2002) demonstrated that male humpbacks preferentially escort females with high reproductive potential, indicating that male–male competition and male mate choice coexist in this species. Pack et al. (2009) demonstrated that larger females attract more male escorts than do smaller females. Male preference for larger females was supported by the finding that larger females produce larger calves than do smaller females (Pack et al. 2009).

In Hawaii, the majority of female humpbacks are observed only once within a breeding season (Craig et al. 2001), and the most common pod composition in which they are found is the male–female dyad (Craig et al. 2002). In fact, most dyads on the breeding grounds are male–female, with fewer male–male and very few female–female dyads (Pomilla & Rosenbaum 2006; Cypriano-Souza et al. 2010; Herman et al. 2011). This suggests that the composition of male–female dyads reflects mate choice in this species. Spitz et al. (2002) measured the lengths of 17 dyad males in the Hawaiian breeding grounds (the sex composition of the dyads containing these males was not reported). Seven (41.2%) were less than 11.3 m long, suggesting probable immaturity based on the relationship between body length and sexual maturity derived by whaling biologists (Omura 1955; Nishiwaki 1959, 1962). Spitz (1999) reported that 12 of 16 dyad females whose lengths were measured were 11.9 m or less, also suggesting probable immaturity (Omura 1955; Nishiwaki 1959, 1962). Consequently, Spitz et al. (2002) proposed that many individuals in dyads are probably sexually immature. However, Clapham et al. (1992) reported that when competitive groups in a North Atlantic breeding area were tracked until only two individuals remained (the number of cases was not given), those two whales were the female and the principal escort. This suggests that these ‘remnant’ dyads consisted of a mature pair.

If size-assortative pairing occurs in humpback male–female dyads, it would explain the observations of both immature male–female pairings and mature male–female pairings in this species. Moreover, the combination of male–male competition and male mate choice has been shown to produce assortative mating in other species (Hardling & Kokko 2005). If the best-quality males select the best-quality females, poorer-quality males may mate with poorer-quality females either because it is an adaptive strategy to avoid costly competition or because this is the only option available (Fawcett & Johnstone 2003; Hardling & Kokko 2005). Thus, we predicted that (1) humpback whales would show size-assortative pairing in dyads, (2) mature females would be more discriminating than mature males in their choice of associate, and (3) large mature males would be more discriminating than small mature males in their choice of female associate.