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Male humpback whales in the Hawaiian breeding grounds preferentially associate with larger females

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The competitive group appears to be a major component of the mating system of the humpback whale, *Megaptera novaeangliae*, bringing together a single female (nuclear animal or NA) and multiple males (escorts) that compete for physical proximity to her. We examined the relation of body size of the NA to the number of attending escorts and, separately, we determined the relation of a female's body size to the size of her calf. Using underwater videogrammetry in Maui waters during 1997–2002, we measured the body length of the NA in each of 42 competitive groups. We also measured the lengths of the mother and her calf in each of 92 mother–calf groups. The number of initial escorts in a competitive group was positively correlated with NA body length. Longer mothers were associated with longer calves, even after accounting for seasonal differences in calf length. We conclude that male humpback whales prefer to associate with larger females and that larger females produce larger calves. Theoretically, larger calves have a greater chance of survival than do smaller calves. The choice of a larger female may therefore increase the reproductive success of an escort that succeeds in mating.

In many species, body size is an honest indicator of female reproductive potential. Larger females are often more fecund and/or better able to produce and rear higher-quality offspring than are smaller females (reviewed in Shine et al. 2006; also see Ralls 1976). Males may therefore preferentially choose to mate with larger females as has been shown in fish (Downhower & Brown 1981; Rowland 1982; Sargent et al. 1986), reptiles (Shine et al. 2006) and terrestrial mammals (Preston et al. 2005). Here, we examine whether male humpback whales, *Megaptera novaeangliae*, show preferences for larger (longer body length) female humpback whales during the breeding season.

Humpback whales are a migratory species with distinct feeding and breeding areas (Chittleborough 1965; Dawbin 1966; Baker et al. 1986; Katona & Beard 1990). In winter and spring months, humpback whales assemble on low-latitude shallow banks and along coastal areas for breeding and calving (Baker et al. 1986; Craig et al. 2003). There, male humpback whales, either singly or in groups, 'escort' (after Herman & Antinoja 1977) females, apparently seeking mating opportunities (the act of mating in humpback whales has never been documented; Clapham 2000; Pack et al. 2002). Female humpbacks produce a single calf on average every 2–3 years (Baker et al. 1987; Barlow & Clapham 1997), and the majority of females do not ovulate while lactating (Chittleborough 1965). Furthermore, some evidence suggests that not all females may migrate to the breeding grounds each year (Brown et al. 1995; Craig & Herman 1997). This confluence of factors results in an operational sex ratio on the breeding grounds heavily biased towards males (Herman & Tavolga 1980), which compete with each other, often intensively, for access to lone females within 'competitive groups'.

A competitive group consists of multiple males and a single female (Tyack & Whitehead 1983; Baker & Herman 1984; Clapham et al. 1992). Some of the males engage one another with threats and direct aggression, such as high-speed charges and body strikes (Baker & Herman 1984; Herman et al. 2008). The aggressing males are typically vying for proximity to the female, with one male, termed the 'principal escort', succeeding but having to defend that position frequently against challengers (Tyack & Whitehead 1983).

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Other males within a competitive group, termed 'secondary escorts' (Tyack & Whitehead 1983), often remain on the periphery and do not directly challenge the principal escort, although they may occasionally aggress towards each other (Herman et al. 2008). The size of competitive groups may range in numbers of males from as few as two to as many as 20 or more. The degree and ferocity of aggression between males appear to increase with group size (Baker & Herman 1984). Competitive groups can persist for hours, during which the group may travel over many kilometres. Although affiliations and disaffiliations are commonly observed (Mobley & Herman 1985), the principal escort and others in the group may remain throughout all or much of that time, evidencing a large investment in both time and, apparently, energy in a single female. Thus, a male strategy seems to be to focus selectively on fewer females rather than on an indiscriminately large number.

Male humpback whales have small testes relative to their body length, in contrast to male bowhead whales, *Balaena mysticetus*, right whales (*Eubalaena* sp.) and grey whales, *Eschrichtius robustus*, suggesting that physical contests between males, rather than sperm competition (Brownell & Ralls 1986), characterize the mating strategy of the male humpback whale. Male–male physical contests generally favour the individual with the larger body size. Spitz et al. (2002) used underwater videogrammetry to measure the body lengths of male humpback whales in various social roles and found that principal escorts were, on average, significantly longer than secondary escorts, single escorts and male partners in dyads. Importantly, individual principal escorts tended to be the longest or second-longest male in their respective competitive group. Spitz et al. (2002) concluded that body size confers an advantage for male humpback whales in competitive groups.

Despite the apparent advantage of male body size, humpback whales show a modest degree (ca. 5%) of reverse body-size dimorphism, probably reflecting selection for large female size to satisfy the metabolic and nutritional needs of lactation (Ralls 1976; Ralls & Mesnick 2002). According to whaling data, mature female humpbacks in the North Pacific average 0.7 m longer than mature males (Nishiwaki 1959, 1962). Because humpback whales, other than nursing calves, fast on the breeding grounds (Nishiwaki 1959; Chittleborough 1965; Dawbin 1966), both males and females must rely on stored body fat accumulated during the summer feeding season to support their metabolic requirements during the winter breeding season. Large body size allows for a greater accumulation of body fat (Calder 1984; Fedak et al. 2002). However, females have the additional metabolic burdens of gestation and lactation that can be offset by increased body size (more fat storage capacity) relative to that attained on average by males. A larger female humpback whale should therefore be better able than a smaller female to support herself and her calf during fasting periods and produce larger calves without sacrificing her own metabolic needs (Fedak et al. 2002). Thus, if bigger mothers are better mothers (Ralls 1976), male humpback whales would benefit by preferentially mating with larger females over smaller ones (see also Clutton-Brock et al. 1988). In the current paper, we used underwater videogrammetry (Spitz et al. 2000) to measure the body length of the female humpback whale within each of many different competitive groups in Hawaiian waters, and related that measurement to the number of escorts accompanying the female. We predicted a positive relationship between female body length and number of escorts. Furthermore, we measured the lengths of mothers and their calves to obtain empirical data on the association of mother size and calf size. We predicted a positive relation between mother length and calf length, even after accounting for seasonal differences in calf length.

METHODS

Study Area and Survey Period

We conducted the study during December–April from 1997 to 2002 in the waters of the Auau, Kalohi and Pailolo channels off West Maui. This area, known as the 'four-island' region, contains one of the densest concentrations of humpback whales in the Hawaiian Islands during winter and spring months (Herman et al. 1980; Mobley et al. 1999).

Procedure

Observation and identification

When weather and sea state permitted, we searched for and approached humpback whales using two small (<8 m) outboard boats. Our observation effort was continuous throughout the day from approximately 0830 hours to 1700 hours in the lee areas between west Maui and north Lanai, comprising approximately 340 km^2.

Groups of whales sighted by observers aboard the vessels were approached for close study without bias towards any particular type of group. As an initial step, an approached group was assigned a number code (1 for the first group of the day, 2 for the second, and so forth) and the number of whales present in the group was estimated. Individual whales in that group were then given temporary 'names' corresponding to the shape of and markings on their dorsal fins (e.g. scar, hook, tall). This labelling method allowed us to recognize the individual whales initially present in the group and refine our count of their numbers. The labels also enabled us to link observed behaviours to particular individuals and, as they dove, to the unique coloration patterns on the ventral surface of their tail flukes (Katona et al. 1979). Identification photographs of individual tail flukes of all or nearly all whales were obtained using 35 mm cameras equipped with 300 mm lenses. The times of occurrence of each observed behaviour and each identification photograph were recorded manually along with the social roles of identified individuals.

A competitive group was defined as a group of three or more adult whales in which one individual male, the principal escort (PE), attempted to maintain close proximity to the lone female, the 'nuclear animal' (NA). The NA was identified through her behaviours (generally passive and nonaggressive), her location in the group (typically forward or central), her spatial and social relation to other whales (usually attended closely by a single whale, the PE, that often aggressed against other whales), and by direct underwater observation of her genital area by a snorkeler (females but not males have a prominent hemispheric lobe caudal to the genital slit; True 1904; Glockner 1983). The PE was identified as the whale defending his position adjacent to the NA against intrusions or challenges by other escorts ('challengers'). Defence was through one or more aggressive actions or displays, such as physically blocking the approach of another whale, blowing streams of bubbles, surfacing with throat pleats inflated, actively chasing a challenger at high speed, or using a body part to strike a challenger (Tyack & Whitehead 1983; Baker & Herman 1984). During focal follows of a competitive group we kept track of each change in group composition (i.e. due to any affiliation or disaffiliation by one or more escorts; see Mobley & Herman 1985) by retaining the same assigned group number but appending this number with a letter code (e.g. 1A for the first change in composition of Group 1, 1B for the second change in composition in Group 1, and so forth). The time of each change and the identities of the whales involved were also recorded. If a disaffiliation of one or more escorts occurred, we remained with the group containing the NA. Generally,