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Habitat preferences by individual humpback whale mothers in the Hawaiian breeding grounds vary with the age and size of their calves

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We investigated whether calf age and calf size influence habitat choice by humpback whale mother–calf pairs in their breeding grounds. During 1997–2008, we conducted focal follows of mother–calf pairs in Hawaiian waters. Tail-fluke identification photographs and calf lengths (measured through videogrammetry) were obtained. Water depth and sea-bed terrain type were derived from GPS data. Identification photographs were matched so that the habitat choices could be established within breeding seasons. Across 72 mother–calf pairs resighted over various intervals within a breeding season, magnitude of depth change between initial and final sightings increased significantly with resighting interval. There was a significant increase from initial depth to final depth for relatively long resighting intervals (27–51 days), but no significant difference for relatively short resighting intervals (2–26 days). Although there was no preference for sea-bed terrain type by mother–calf pairs at their initial sighting, there was a preference for rugged terrain at their final resighting. A resource selection model indicated that the relative probability of a location being used by a mother–calf pair increased (as a function of water depth and rugged sea-bed terrain type) from initial to final sighting; a finding supported by subsequent tests of habitat preference versus availability. For 96 measured calves, calf length and water depth were positively correlated, even when ordinal day of measurement was controlled for statistically; a finding confirmed by a general linear model that simultaneously investigated the relationship between water depth, sea-bed terrain type, number of escorts, ordinal day and calf size. Thus, both calf age and size influence habitat choice by mother–calf pairs in their breeding grounds. The movement of mothers and their maturing calves into deeper waters where they favour rugged sea-bed terrain appears to be part of a suite of behavioural changes during the pre-migratory phase of residency in the breeding grounds.

In a variety of species in which newborns remain dependent on their mothers beyond parturition, females with offspring often segregate themselves into habitats that are different from those used by females without offspring (e.g. Ciuti, Bongi, Vassale, & Apollonio, 2006; Craig, Herman, Pack, & Waterman, 2014; Lent, 1974; Walker, Parker, & Gillingham, 2006; Wolf, Kauermann, & Trillmich, 2005). For mammals, such segregation may be motivated by predator avoidance (e.g. Ciuti et al., 2006; Main, Weckerly, & Bleich, 1996; Pinard, Dussault, Ouellet, Fortin, & Courtois, 2012; Rachlow & Bowyer, 1998; Walker et al., 2006), access to better food resources (including fresh water for land-dwelling mammals) (Rachlow & Bowyer, 1998), limitations in offspring mobility and

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activity budgets (Grignolio, Rossi, Bertolotto, Bassano, & Apollonio, 2007), avoidance of harassment by males prospecting for mating opportunities (e.g. Craig et al., 2014; Wolf et al., 2005), or promotion of mother–offspring bonding (Lent, 1974; Mann & Smuts, 1998; Ozoga, Verme, & Bienz, 1982; Schwede, Hendrichs, & McShea, 1993). In some cases, two or more of these factors may exert conflicting pressures. For example, females with recent offspring may relocate to habitats that reduce predation risk to offspring but are also of low productivity, thus compromising their energy intake (e.g. Ciuti et al., 2006). A female's habitat use may also change in relation to her recent offspring's growth, maturation and behaviour as well as her own need to replenish resources or seek mates (e.g. Bon, Joachim, & Maublanc, 1995; Costelloe & Rubenstein, 2015; Grignolio et al., 2007; Jones & Swartz, 1984; Thomas & Taber, 1984). Here, we investigate changes in the habitat use of individually identified humpback whale, *Megaptera novaeangliae*, mothers as a function of the relative age and size of their calves.

Humpback whales are a migratory species with distinct areas for feeding and breeding typically separated by thousands of kilometres (Baker et al., 1986; Chittleborough, 1965; Dawbin, 1966; Katona & Beard. 1990). In summer months, the whales inhabit high-latitude productive waters where they feed on krill and small schooling fish. During winter and spring months, humpbacks of both sexes and all age classes inhabit lower-latitude tropical waters where they calve (females on average produce a single calf every 2–3 years; Baker, Perry, & Herman, 1987; Barlow & Clapham, 1997), rear young and perform behaviours related to mating (summarized in Clapham, 1996, 2000). In these so-called breeding grounds, feeding (other than by nursing calves) is suspended (Chittleborough, 1965).

A humpback whale calf's habitat use is inextricably linked to that of its mother while in the breeding grounds during its first months of life. As in some ungulate and marsupial (macropod) species, humpback whale offspring exhibit a 'following' (versus a 'hiding') strategy (Fisher, Blomberg, & Owens, 2002; Lent, 1974), typically remaining within 50 m of their mothers during both travel and resting periods (Cartwright & Sullivan, 2009a; Szabo & Duffus, 2008). Of the factors favoured by Fisher et al. (2002) in the evolution of a following strategy in ungulates and macropods, the one that appears most applicable to humpback whales is raising young in an open habitat where hiding is less favoured because of increased predation as well as harassment from conspecifics. Fisher et al. (2002) also promoted the hypothesis that a following strategy is typically associated with delayed weaning because following offspring expend more energy on movement than hiding/sedentary offspring. Humpback whale calves are reared in the open ocean, and weaning occurs after a lactation period of approximately 10.5 months (Chittleborough, 1958). In addition to reducing predation and harassment pressure, following among humpback calves may have evolved to promote the development of muscular myoglobin stores, which are extremely low in neonates but increase significantly by the start of migration to the feeding grounds because following requires more energy than hiding (Cartwright et al., 2016). Muscular myoglobin is important in a humpback's ability to perform the extended aerobic dives typically employed during foraging behaviour and other activities (Kooyman & Ponganis, 1998; Ponganis, 2011; Snyder, 1983).

It has been well established in several populations of humpback whales that mother–calf pairs favour shallow water habitats in the breeding grounds (Betancourt, Herrera-Moreno, & Beddall, 2012; Craig et al., 2014; Ersts & Rosenbaum, 2003; Félix & Botero-Acosta, 2011; Guidino, Llapapasca, Silva, Alcorta, & Pacheco, 2014; Herman & Antinoja, 1977; Smultea, 1994). For example, shore-based observations of humpback whales off Hawaii Island by Smultea (1994) revealed that pods containing a calf occupied waters that were significantly shallower than pods without a calf. Smultea (1994) suggested several potential reasons for the segregation of mother–calf pairs into shallow waters, including avoidance of harassment by sexually active males, avoidance of turbulent waters and avoidance of predators (e.g. killer whales, *Orcinus orca*, and tiger sharks, *Galeocerdo cuvier*). Recently, Craig et al. (2014) presented substantial evidence to support the harassment avoidance hypothesis, using shore-based theodolite tracking of humpback whales off the west coast of Maui, Hawaii. In addition to demonstrating a significant shallow water preference by pods containing a calf, as compared to noncalf pods, Craig et al. (2014) showed that mother–calf pairs without a male escort occupied significantly shallower waters than those containing one or more male escorts, that the number of males escorting a mother–calf pair decreased progressively with decreasing water depth and that speed of travel (and thus energy expenditure) increased as the number of male escorts increased. Craig et al. (2014) were able to discount predator avoidance and access to sheltered waters as potential explanations for their results; instead they concluded that mothers seek shallow waters to avoid the costs of male harassment.

Sea-bed terrain has also been investigated as a potential factor influencing habitat preferences of humpback whale mother–calf pairs in the breeding grounds. Cartwright et al. (2012) conducted boat-based transect surveys off the west coast of Maui and reported a preference by mother–calf pairs for waters associated with rugged sea-bed terrain rather than flat sea-bed terrain. They attributed this to a generalized preference of mothers for shallow water habitats, noting that the rugged terrain in their study area, composed of ridges of drowned karst reef, tended to be slightly shallower than flat terrain, which was composed of sandy basins (Grigg et al., 2002). However, because the surveys conducted by Cartwright et al. (2012) all took place in March, which is relatively late in the breeding season (Baker & Herman, 1981; Mobley, Bauer, & Herman, 1999), it is possible that many of the calves in the survey sample were beyond the neonate stage. Thus, the findings by Cartwright et al. (2012) may largely reflect habitat preferences of mothers with older calves.

Despite advances in the understanding of some of the factors associated with habitat preferences by humpback whale mother–calf pairs in the breeding grounds, the potential influences of calf age and calf size have not been considered. This is because longitudinal data from individually identified humpback whale mother–calf pairs over the course of the breeding season have rarely been examined with respect to habitat use (Craig & Herman, 2000). In this paper we investigated how individually identified humpback whale mothers in the breeding grounds vary their habitat use in relation to the relative age and size of their calves.

To investigate the influence of calf age on habitat selection, we examined whether there were any significant changes in habitat use by individual mother–calf pairs resighted over varying periods of time within a breeding season. To the extent that a resighting of a mother–calf pair within a breeding season reflects the presence of an older calf (compared to an initial sighting), this analysis allowed us to investigate whether habitat use by a humpback whale mother–calf pair changes as the calf within this pair ages. In later stages of calf development, grey whale, *Eschrichtius robustus*, mother–calf pairs relocate into deeper water habitats, with some travelling outside of breeding lagoons (Jones & Swartz, 1984; Mate, Lagerquist, & Urban-Ramirez, 2003; Swartz, 1986). Based on this finding in another mysticete species, we hypothesized that calf age affects the ocean depth used by mother–calf pairs. We predicted that as the time interval between the initial and final sightings of a mother–calf pair increases (reflecting a calf of increasing age), the magnitude of depth change between initial and final sightings would also increase. As a corollary to this hypothesis, we predicted