

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

Adam A. Pack<sup>a,b,c,\*</sup>, Louis M. Herman<sup>a,d</sup>, Scott S. Spitz<sup>a</sup>, Siri Hakala<sup>e</sup>, Mark H. Deakos<sup>d</sup>, Elia Y. K. Herman<sup>a,f</sup>

<sup>a</sup>The Dolphin Institute, Honolulu, HI

<sup>b</sup>Department of Psychology, University of Hawaii at Hilo, HI

<sup>c</sup>Department of Biology, University of Hawaii at Hilo, HI

<sup>d</sup>Department of Psychology, University of Hawaii at Manoa, HI

<sup>e</sup>Southwest Fisheries Science Center, La Jolla, CA

<sup>f</sup>Nicholas School of the Environment and Earth Sciences, Duke University, Durham, NC

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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.

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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 & Antinaja 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).

\* Correspondence: A. A. Pack, Department of Psychology, University of Hawaii at Hilo, 200 West Kawili Street, Hilo, HI 96720, U.S.A.

E-mail address: [pack@hawaii.edu](mailto:pack@hawaii.edu) (A.A. Pack).

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<sup>2</sup>.

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,

a competitive group of whales was tracked until, to the extent possible, all individuals had been identified photographically and the social roles of individual animals had been determined (NA, principal escort, secondary escort). The length of observation of a competitive group typically ranged from 30 to 60 min but could last as long as several hours. However, to control for differences in the duration of focal follows, we only used data on the initial number of escorts, defined as the number of escorts recorded prior to any changes in association with the NA. For our analysis of female length versus number of escorts, this reduced the number of eligible measured NAs from 42 to 41 because one NA was initially sighted in the company of a single escort before being joined by a second escort.

Mother–calf groups were defined as any size group of whales in which a mother and calf were present. Calves are easily identified by their small size relative to adults (typically one-third of adult length). A mother was identified by consistent close proximity to a calf. On the winter grounds, humpback whale mother–calf pairs do not interact with each other and may be found alone or in association with one or more escorts (Herman et al. 1980; Clapham 1996).

When the whales under observation were stationary, milling or travelling slowly, we deployed a swimmer equipped with mask, snorkel and fins, and carrying a high-frequency (200 or 400 kHz) hand-held ‘flashlight-type’ sonar device (Speedtech Depthmate, Speedtech Instruments, Great Falls, VA, U.S.A.) and a digital video camera (Sony DCR-TRV-7, Sony Corp, New York, NY, U.S.A.) in an underwater housing (Jay-Mar VM-6000, Jay-Mar Engineering, San Pedro, CA, U.S.A.). The goals of the swimmer were to obtain video records of the whales suitable for subsequent length analyses, to make underwater visual observations and video records of behaviour and social interactions, and to determine the sex of individual whales.

#### Measuring body length

We used underwater videogrammetry (Spitz et al. 2000) to measure the lengths of individual NAs, mothers and calves. This technique has been used successfully previously to measure the lengths of individual male humpback whales in different behavioral roles (Spitz et al. 2000, 2002; Pack et al. 2002). The technique requires a lateral image of the full length of a whale recorded on video, a measure of the distance from the camera to the whale, and knowledge of the field of view of the camera. Full details are available in Spitz et al. (2000). Briefly, the swimmer obtains video records of the whale when the whale is away from the surface (so as to avoid false sonar readings from surface reflections) and positioned perpendicular to the longitudinal axis of the camera, such that the full image of the whale is within the camera’s field of view. Multiple independent measurements are obtained as the swimmer moves relative to a stationary whale, or when the whale moves and the swimmer repositions himself or herself, or when the whale swims off and then slows down again, presenting another opportunity for the boat to approach and deploy the swimmer. Distance to the whale is measured with the sonar device multiple times as the swimmer continues filming. The sonar device when activated records and displays in a digital readout the distance to the whale in tenths of feet and also produces a click sound that is captured by the acoustic component of the video record. The digital readout is locked on the display screen of the sonar device and is then held in front of the camera to obtain a permanent record of the distance. The objective of the swimmer is to obtain at least three independent measures of each individual whale to increase the reliability of measurement, although this was not always possible. However, Spitz et al. (2002) demonstrated the accuracy of the videogrammetric technique even when only one measurement is obtained.

#### Data Analyses

All tail fluke identification photographs in the entire data set were compared against each other to determine whether any NAs, mothers or calves had been photographed on more than one day. If a whale was photographed on multiple days (rare), only the data from the initial day were used in the current analyses. Further comparisons of all identification photographs of NAs and mothers were made against our archival catalogue of North Pacific humpback whale tail fluke photographs to determine the sighting histories of whales that had been photographed on more than one occasion. This catalogue (the early portion of which is published in Perry et al. 1988) consists of over 21 000 identification photographs of approximately 5000 individual humpback whales dating back to 1976.

For videogrammetric analysis, individual frames in which the click sound from the sonar device was heard were judged for suitability of the captured image. To qualify for measurement, a full body image of a whale must be visible, there must be no curvature of the body and the camera axis must be perpendicular, or nearly so, to the whale’s body and as close to the body midline as possible. All images were judged for suitability and measured by one of two individuals (co-authors S.S.S. and S.H.) using Adobe Photoshop software using basic photogrammetric principles as described in Spitz et al. (2000). These individuals had been trained initially on the same subset of whale images to ensure consistency in measurement. During measurements, they were ‘blind’ to the number of escorts present. For each whale measured, the mean of the independent measurements for that individual represented the whale’s final measured length. Tomilin (1967), reporting on Soviet catches of North Pacific humpback whales in the 1930s, measured a female that was pregnant for the first time at 9.8 m. Therefore, all NAs and mothers whose measured lengths were at least this length were included in the database.

The initial number of escorts in each competitive group and the length data for each uniquely identified NA, mother and calf were organized and analysed in Excel and SPSS.

## RESULTS

We measured the body lengths of the NA in each of 42 competitive groups and determined the number of escorts in each group. Additionally, we measured the lengths of the mother and her calf in each of 92 mother–calf groups. Table 1 gives the mean

**Table 1**

Length measurements of female humpback whales, *Megaptera novaeangliae*, in the role of nuclear animal or mother when measured, and length measurements for calves of both sexes

Social role	No. independent measures	No. whales	Length (m)				
			Mean	Median	CI	Range	Mean CV
Nuclear animal	1	20	12.18	12.18	±0.34	10.66–13.49	NA
	2	9	12.43	12.54	±0.58	11.24–13.96	0.024
	3 or more	13	12.16	12.13	±0.47	10.29–13.49	0.035
Overall		42	12.23	12.16	±0.24	10.29–13.96	0.03
Mother	1	52	12.34	12.26	±0.24	10.68–14.75	NA
	2	21	12.77	12.75	±0.25	11.65–13.88	0.034
	3 or more	19	12.48	12.52	±0.35	11.14–13.92	0.029
Overall		92	12.47	12.47	±0.17	10.68–14.75	0.03
Calf	1	42	5.29	5.21	±0.20	3.96–6.41	NA
	2	18	5.20	5.26	±0.32	3.77–6.50	0.038
	3 or more	32	5.06	5.11	±0.19	3.80–6.06	0.047
Overall		92	5.19	5.18	±0.13	3.77–6.50	0.044

CI = 95% confidence interval; CV = coefficient of variation.

and median lengths of the NAs, mothers and calves, grouped by the number of independent measurements obtained, 1, 2 or 3 or more (see *Methods*). Each of the whales measured was a unique individual, based on tail fluke photographic identification data. The mean coefficient of variation (CV) is the arithmetic mean of individual CVs for whales measured independently more than once during the same encounter in a day. The means of the CVs were uniformly low ( $<0.05$ ), indicating that the variability in measurement was low and comparable across groups despite the very different mean lengths of adults and calves and despite the number of independent measurements obtained. As further evidence for the reliability of the length measurements obtained, *Table 2* shows the mean lengths for NAs, mothers and calves measured three or more times based on the first measurement only, versus the first and second measurements combined, versus the mean lengths for all available measurements. A general linear model repeated measures analysis indicated no significant difference between the lengths derived across the three types of measures for 13 NAs ( $F_{2,24} = 0.318$ ,  $P = 0.730$ ), 19 mothers ( $F_{2,36} = 0.025$ ,  $P = 0.975$ ) and 32 calves ( $F_{2,62} = 0.587$ ,  $P = 0.559$ ) for which these types of data were available. These results are consistent with earlier findings on the validity of using single measurements of lengths of individual male humpback whales (Spitz et al. 2002).

We also examined whether there were any biases in data collection for those whales whose lengths we measured only once, versus those measured exactly twice, versus those measured three or more times (see *Table 1* for means). A one-way ANOVA showed no significant differences in the obtained lengths for NAs ( $F_{2,39} = 0.356$ ,  $P = 0.702$ ), mothers ( $F_{2,89} = 2.16$ ,  $P = 0.122$ ) or calves ( $F_{2,89} = 1.17$ ,  $P = 0.315$ ). Thus, there were no biases in those animals that were measured once, twice or multiple times. Therefore, the final lengths of individual whales used in all subsequent analyses included those measured once as well as the mean of the independent measures of those individuals measured more than once.

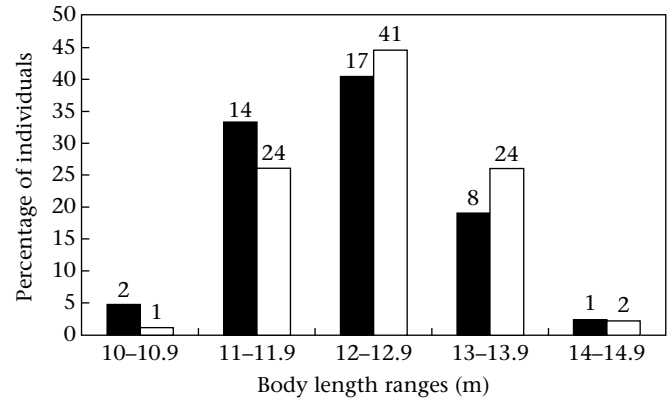
#### Lengths of Nuclear Animals and Mothers

*Figure 1* shows the percentage of NAs and mothers whose body lengths were within particular ranges. The histogram reveals considerable overlap between the relative percentages of NAs and mothers within each range of lengths and roughly approximates a normal distribution. *Figure 2* shows the distribution of individual body lengths for NAs and mothers. The mean NA ( $12.23 \pm 0.13$  m) and maternal ( $12.47 \pm 0.08$  m) body lengths were not significantly different ( $t$  test:  $t_{132} = -1.59$ ,  $P = 0.11$ ). Furthermore, there was no significant difference between the distribution of numbers of mothers and numbers of NAs above and below the combined median

**Table 2**

Mean lengths  $\pm$  95% confidence intervals (CI) for all first measurements alone, for first and second measurements combined and for all available measurements of nuclear animals, mothers and calves that were measured three or more times

Social role	Type of independent measures	Number	Length (m)	
			Mean	CI
Nuclear animal	1st only	13	12.21	$\pm 0.61$
	Mean of 1st and 2nd	13	12.25	$\pm 0.52$
	Mean of all available	13	12.16	$\pm 0.47$
Mother	1st only	19	12.49	$\pm 0.46$
	Mean of 1st and 2nd	19	12.49	$\pm 0.37$
	Mean of all available	19	12.48	$\pm 0.36$
Calf	1st only	32	5.10	$\pm 0.21$
	Mean of 1st and 2nd	32	5.09	$\pm 0.18$
	Mean of all available	32	5.06	$\pm 0.19$



**Figure 1.** Histogram showing the percentage of humpback whale nuclear animals (solid bars) and mothers (open bars) whose lengths as determined through videogrammetry were within particular ranges. The number of individuals within a particular range is shown above each bar.

length (median = 12.38 m,  $N = 134$ ; chi-square test:  $\chi^2_1 = 1.70$ ,  $P = 0.19$ ).

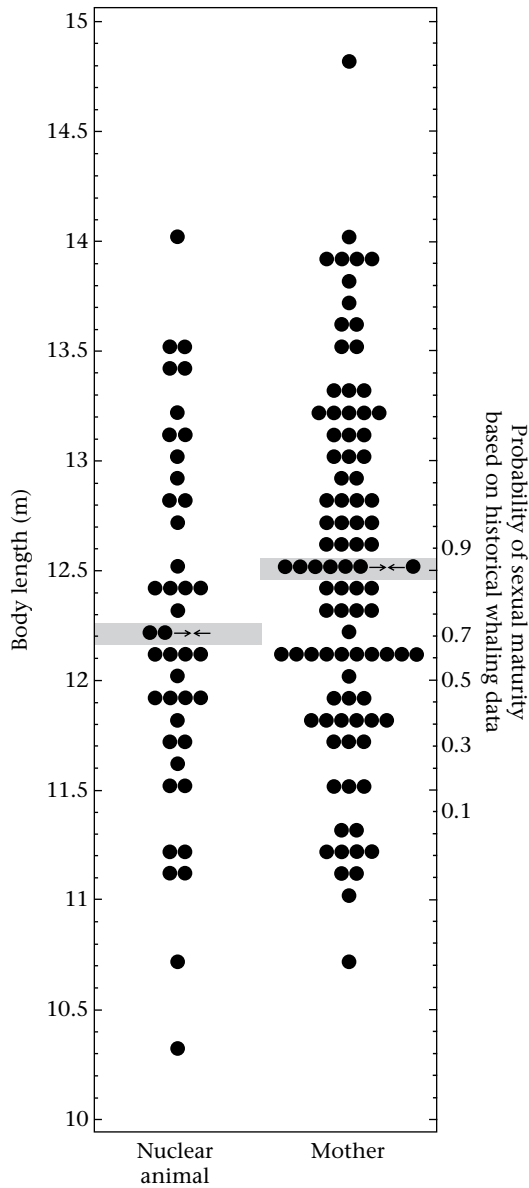
*Figure 3* shows the body lengths at which female North Pacific humpback whales attain sexual maturity, based on measurements of female carcasses by Japanese whaling biologists in the 1950s and 1960s: 108 by Nishiwaki (1959), 59 by Nishiwaki (1962) and 100 by Omura (1955). Females with ovaries containing neither new nor old corpora luteum were defined as immature (Nishiwaki 1959, 1962). The data points in *Fig. 3* are based on the combined Japanese data for lengths between 10.67 m (35 ft) and 13.11 m (43 ft). All whales 10.67 m or shorter ( $N = 24$ ) were found to be sexually immature and all whales 13.11 m or longer ( $N = 96$ ) were found to be sexually mature. The smallest whale that was determined to be sexually mature by Japanese biologists was one of 12 measured at 10.97 m. For our data, 91 of the 92 mothers (99%) and 40 of the 42 nuclear animals (95%) were measured at lengths above 10.97 m. As we had done previously for male humpback whales (Spitz et al. 2002), an empirical fit to the Japanese whaling data for females was made using the cumulative normal probability density

$$p = F(x|\mu, \sigma) = \frac{1}{\sigma\sqrt{2\pi}} \int_{-\infty}^x e^{-\frac{(x-\mu)^2}{2\sigma^2}} dx$$

function where  $\mu = 11.97$ ,  $\sigma = 0.48$ , and  $x$  is body length. We extrapolated from this sigmoid function the probability values of sexual maturity ranging from 0.1 to 0.9 that were associated with whales of different body lengths. These probability values were then plotted on a secondary Y axis in *Fig. 2*. We found that 62% of NAs and 73% of mothers were of lengths with probabilities of sexual maturity of 0.5 or greater. The median lengths of NAs (12.2 m) and mothers (12.5 m) were associated with 0.7 and 0.9 probabilities of sexual maturity, respectively. The smallest NA measured was 10.29 m, a length associated with a 0.00023 probability of sexual maturity and 2.37 standard deviations from the mean length of NAs of 12.23 m. Four independent measures were obtained of this whale and the CV of 0.01 indicated a high degree of reliability in measurement. Because this NA was longer than the minimum length of a pregnant North Pacific female humpback whale reported by Tomilin (1967) (see *Methods*), it was retained in the database.

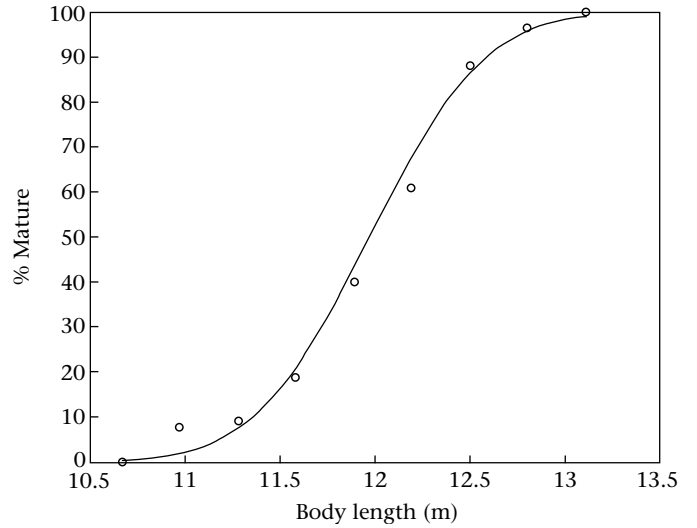
#### Relationship of Length of Nuclear Animals, Number of Escorts and Time of Measurement

The number of escorts associated with an NA ranged from 2 to 15. *Figure 4* plots the body length of each NA versus her initial



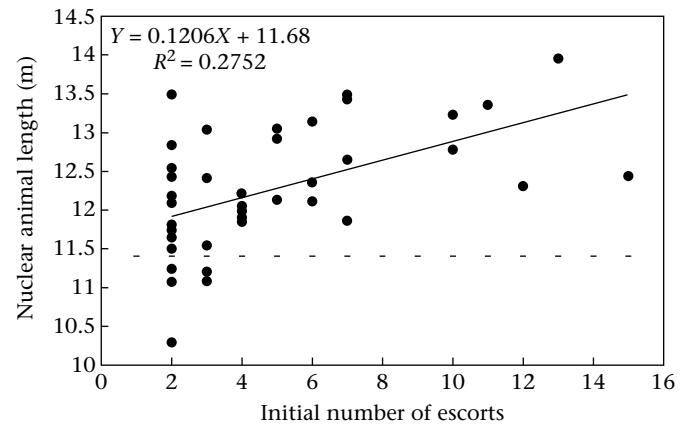
**Figure 2.** The distribution of measured lengths of individual female humpback whales occupying the role of nuclear animal (a calfless female in a competitive group of males) or mother (a female with her calf either alone or escorted by one or more males). Each shaded bar represents the mean of the distribution. Arrows within shaded bars indicate the location of the median. The secondary Y axis shows the probabilities (0.1–0.9) of sexual maturity associated with particular lengths as based on measurements of North Pacific female humpback whales by Japanese whaling biologists (see text).

number of escorts. A multiple regression analysis showed a significant positive correlation between NA length and initial number of escorts ( $R^2 = 0.28$ ;  $F_{1,39} = 14.81$ ,  $P = 0.0004$ ). Herman et al. (1980) and Baker & Herman (1984) showed that as the breeding season of humpback whales in Hawaiian waters progresses, both the size of humpback whale groups and the percentage of groups engaged in aggression (i.e. competitive groups) increases. It is therefore possible that the time of the season that we measured NAs was related to the body length of the whales measured and the number of escorts observed. Indeed, Figs 5 and 6 show positive relationships, respectively, between the ordinal date (days since 1 January, with 1 January counted as 1, 2 January as 2, and so forth) of data collection and NA length ( $R^2 = 0.10$ ;  $F_{1,39} = 4.34$ ,  $P = 0.04$ ) as well as number of initial escorts ( $R^2 = 0.11$ ;  $F_{1,39} = 4.92$ ,  $P = 0.03$ ).

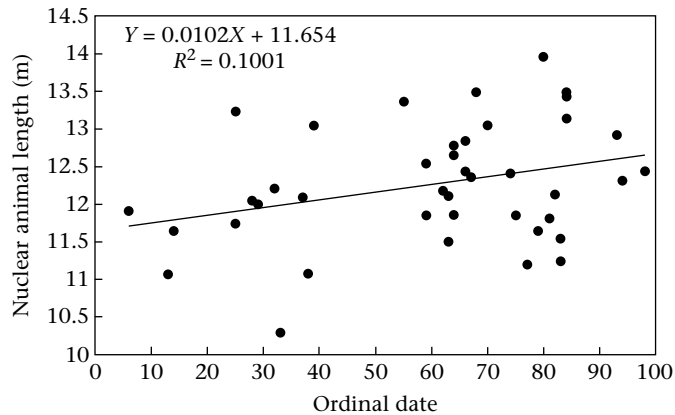


**Figure 3.** A fitted curve showing the percentages of North Pacific female humpback whales that were estimated to be sexually mature as a function of body length, based on data of the association of the lengths of individual North Pacific female humpback whales with their sexual maturity as determined by whaling biologists. Data points represent pooled data from Nishiwaki (1959, 1962) and Omura (1955).

To determine whether the relationship between NA length and number of initial escorts was a function of the time of season, a multiple linear regression analysis was conducted. Numbers of initial escorts in competitive groups were regressed on NA lengths and ordinal date. These two predictors accounted for about one-third of the variance in numbers of escorts ( $R^2 = 0.31$ ), which was significant ( $F_{2,38} = 8.41$ ,  $P = 0.001$ ). NA length had a significant effect on number of escorts when ordinal date was held constant (standardized regression coefficient:  $\beta = 0.47$ ,  $P = 0.002$ ). However, when NA length was held constant, the effect of ordinal date on number of escorts was not significant ( $\beta = 0.19$ ,  $P = 0.196$ ). NA lengths were then regressed on numbers of initial escorts and ordinal date. These two predictors accounted for about one-third of the variance in NA lengths ( $R^2 = 0.30$ ), which was significant ( $F_{2,38} = 8.05$ ,  $P = 0.001$ ). Number of escorts had a significant effect on NA length when ordinal date was held constant ( $\beta = 0.47$ ,  $P = 0.002$ ). When number of escorts was held constant, the effect of



**Figure 4.** Scatter plot of the measured length of each nuclear animal by her initial number of escorts. The regression line fitting the data is shown together with the regression equation and the  $R^2$  value. The horizontal dashed line at 11.4 m represents the body length at which there is a probability of sexual maturity of 0.1 based on historical whaling data (Omura 1955; Nishiwaki 1959, 1962).

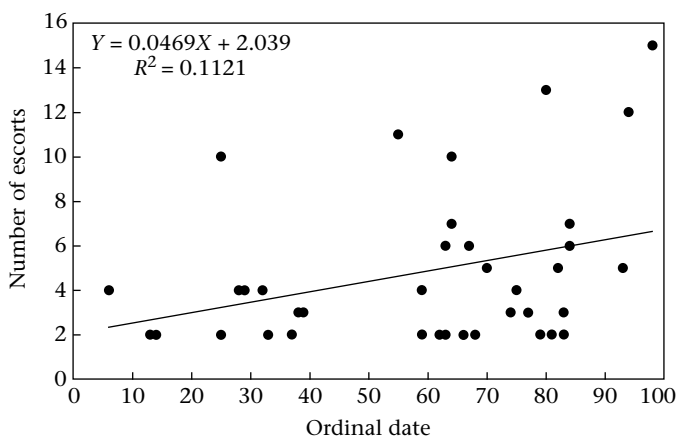


**Figure 5.** Scatter plot of the measured length of each nuclear animal by the ordinal date of its measurement. The regression line fitting the data is shown together with the regression equation and the  $R^2$  value.

ordinal date on NA length was not significant ( $\beta = 0.16$ ,  $P = 0.279$ ). These results demonstrate the validity of the relationship between NA length and number of escorts and that this relationship is independent of ordinal date.

#### Sexual Maturity of Nuclear Animals

Our analyses indicated that the lengths of all but two NAs were greater than the minimum length of 10.97 m for sexual maturity of North Pacific female humpback whales reported by Japanese biologists (Omura 1955; Nishiwaki 1959, 1962), and the lengths of all the NAs exceeded the length of the shortest pregnant female measured by Soviet biologists (Tomilin 1967). However, it is possible that some of the smaller NAs that we measured were nevertheless sexually immature. If so, then the positive relationship we observed between the length of an NA and her number of escorts could reflect sexually mature females attracting greater numbers of escorts than sexually immature females. To control for the maturity level of the NA, we identified those NAs with a sighting history that allowed us to confidently term them as sexually mature. Table 3 lists available sighting histories of the NAs based on matches of tail fluke identification photographs to our archival catalogue. Seventeen of the 41 NAs (41%) were sighted on more than one occasion across years. Fourteen of these 17 (82%) were



**Figure 6.** Scatter plot of the number of initial escorts in each competitive group by the ordinal date of its measurement. The regression line fitting the data is shown together with the regression equation and the  $R^2$  value.

**Table 3**

Sighting histories of measured nuclear animals that were photographed prior to and/or later than their date of measurement ( $N = 17$ )

Whale number	Year measured	Body length (m)	Role (others in group)	Prior sightings	Role (others in group)	Later sightings	Role (others in group)
11969	1998	11.85	NA (4E)	—	—	2002	M (C,E)
308*	1999	13.43	NA (7E)	1983	M (C,E)	—	—
1798*	1999	12.13	NA (5E)	1987	A (2A)	—	—
1842*	1999	13.36	NA (8E)	1986	A (—)	—	—
12931*	1999	12.09	NA (2E)	—	—	2000	M (C,E)
13426*	1999	11.54	NA (3E)	1996	M (C,E)	2001	M (C,E)
				1998	M (C,2E)	2004	M (C,4E)
13608*	1999	13.14	NA (6E)	1997	M (C)	—	—
13923*	2000	11.74	NA (2E)	2000	M (Y)	—	—
14139*	2000	11.85	NA (4E)	—	—	2001	M (C,E)
14613	2000	11.64	NA (2E)	1996	A (1A)	—	—
				1999	NA (5E)	—	—
14722	2000	12.41	NA (3E)	—	—	2005	M (C,E)
14757*	2000	11.20	NA (3E)	1997	M (C)	—	—
				1998	A (1A)	—	—
14779*	2000	11.24	NA (2E)	1988	A (1A)	—	—
14836*	2000	12.92	NA (5E)	1984	A (1A)	—	—
				1998	M (C,E)	—	—
15475*	2001	12.43	NA (2E)	1987	M (C)	—	—
				1997	NA (2E)	—	—
				1998	M (C,E)	—	—
1579*	2002	11.86	NA (7E)	1991	A (2A)	2005	A (1A)
				1997	A (2A)	2006	M (C,1E)
16115*	2002	13.23	NA (10E)	1999	NA (3E)	2003	M (C,2E)

NA = nuclear animal; M = mother; C = calf; Y = yearling; E = escort; A = adult.

Individual whales are identified by their whale sighting number.

Within each cell of columns 4, 6 and 8, the behavioural role of the individual appears, followed, in parentheses, by the numbers and roles of other individuals in the group.

\* Whales of known or highly probable sexual maturity based on their being sighted with a calf in a prior year or within 2 years of being seen as an NA, or being at least 10 years of age (see text).

determined to be sexually mature or to have a high likelihood of sexual maturity through one or more of three lines of evidence: (1) the NA was sighted earlier than the date of measurement as a mother (i.e. either accompanied by a calf or a yearling; only yearlings to which the adult female behaved maternally as it would to its calf, for example, shielding the yearling or stroking it with the female's pectoral fin, were considered); (2) the NA was sighted with a calf in the year following the year it was measured (indicating that in the year it was measured it became pregnant and was therefore sexually mature); and (3) the span of years from an earlier sighting to the year in which the NA was measured exceeded 10 years (the mean age of attainment of sexual maturity in female humpbacks is 5 years of age and thus it is reasonable to assume that a whale older than 10 years is sexually mature; see Chittleborough 1965; Clapham 1992). Seven of the 14 NAs were sighted earlier than the date of measurement either with calf ( $N = 6$ ) or with yearling ( $N = 1$ ). Three other NAs were sighted with a calf the year following the year they were measured. Seven NAs (including four NAs not in the previous two categories) were sighted over spans of greater than 10 years prior to the year they were measured (mean span = 13.4 years, range 11–16 years). Using only these 14 NAs that we could confidently conclude were sexually mature, we conducted a multiple regression analysis in which numbers of initial escorts in competitive groups were regressed on NA lengths and ordinal date. These two predictors accounted for slightly over half of the variance in numbers of escorts ( $R^2 = 0.56$ ), which was significant ( $F_{2,11} = 6.86$ ,  $P = 0.012$ ). Length of known mature NAs had a significant effect on number of escorts when ordinal date was held constant ( $\beta = 0.74$ ,  $P = 0.004$ ). Again however, when NA length was held constant, the effect of ordinal date on number of escorts was not significant ( $\beta = -0.10$ ,  $P = 0.648$ ). Lengths of known mature NAs were then regressed on numbers of initial

escorts and ordinal date. These two predictors accounted for more than half of the variance in lengths of known mature NAs ( $R^2 = 0.55$ ), which was significant ( $F_{2,11} = 6.68$ ,  $P = 0.013$ ). Number of escorts had a significant effect on NA length when ordinal date was held constant ( $\beta = 0.75$ ,  $P = 0.004$ ). When number of escorts was held constant, the effect of ordinal date on NA length was not significant ( $\beta = 0.05$ ,  $P = 0.810$ ). Thus, our finding that male humpback whales preferentially associated with larger females also held when we considered only NAs that were known to be sexually mature.

### Calf Lengths

Calf lengths ranged from 3.77 to 6.50 m (mean = 5.19 m, median = 5.18 m). Nishiwaki (1959) estimated the range of mean birth lengths of North Pacific humpback whale calves as 3.96–4.27 m based on measurements of the lengths of fetuses of pregnant whales caught in the North Pacific (cf. Clapham et al. 1999 for a slightly higher upper limit). Eighty-six of the 92 calves (93.5%) that we measured were longer than Nishiwaki's upper value for mean birth length, suggesting that they were beyond the neonate stage. We plotted the length of each calf versus the ordinal date of its measurement (Fig. 7). There was a positive correlation between calf length and ordinal date ( $R^2 = 0.09$ ;  $F_{1,90} = 8.98$ ,  $P = 0.004$ ). The relatively low positive slope probably reflects the wide range of dates on which birthing occurs, but with more births occurring earlier in the season than later (Nishiwaki 1959).

### Relationship of Length of Mothers, Length of Their Calves and Time of Measurement

Figure 8 plots the length of each mother against the length of her calf. There was a positive correlation between mother length and calf length ( $R^2 = 0.194$ ;  $F_{1,90} = 21.59$ ,  $P < 0.0001$ ). That is, larger mothers were associated with larger calves. However, as noted earlier, there was also a positive correlation between calf length and time of the season of measurement. When we regressed calf lengths on mother lengths and ordinal date, these two predictors accounted for slightly over one quarter of the variance in calf lengths ( $R^2 = 0.26$ ), which was significant ( $F_{2,89} = 15.60$ ,  $P < 0.001$ ). Each of the predictors, mother length ( $\beta = 0.41$ ,  $P < 0.001$ ) and ordinal date ( $\beta = 0.26$ ,  $P = 0.006$ ) had significant effects on calf length when the alternate predictor was held constant.

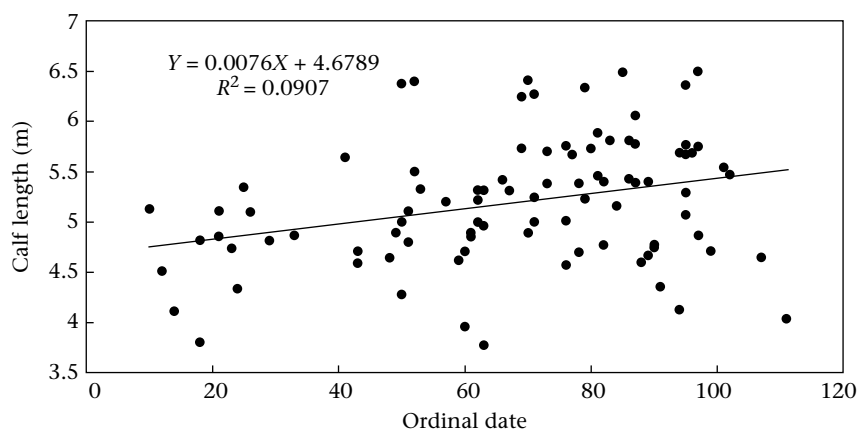
To help determine whether larger mothers were producing larger calves than were smaller mothers, we examined the length of

mothers as a function of the time of season they were measured. In theory, a positive correlation between mother length and calf length could occur if larger mothers tended to be sampled later in the season when their calves had naturally grown larger. We regressed mother lengths on calf lengths and ordinal date. These two predictors accounted for slightly less than one-fifth of the variance in mother lengths ( $R^2 = 0.19$ ), which was significant ( $F_{2,89} = 10.73$ ,  $P < 0.001$ ). Although calf length had a significant effect on mother length when ordinal date was held constant ( $\beta = 0.45$ ,  $P < 0.001$ ), the opposite was not true. That is, when calf length was held constant, the effect of ordinal date on mother length was not significant ( $\beta = -0.03$ ,  $P = 0.751$ ). These results show that larger mothers were indeed producing larger calves irrespective of the ordinal date of our measurements.

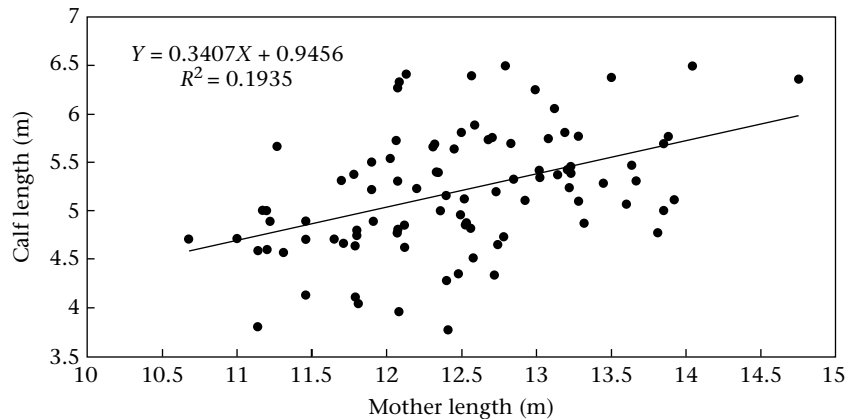
### DISCUSSION

Our findings give support to the hypothesis that male humpback whales stand to benefit by preferentially associating (and presumably mating) with larger females than with smaller females. This was shown most clearly by the strong positive relationship between the length of the nuclear animal (the lone female) in a competitive group and the number of accompanying escorts. This relationship was robust and was not significantly affected by the time of season (ordinal date) on which measurements were obtained, even though group size and aggression typically increase as the breeding season advances (Herman et al. 1980; Baker & Herman 1984). Furthermore, the relationship held even for a subset of NAs whose sexual maturity was unequivocal. It seems probable, however, that all or nearly all NAs were sexually mature, based on three lines of circumstantial evidence: (1) all but two NAs were of lengths greater than the minimum length for sexual maturity determined by Japanese whaling biologists (Omura 1955; Nishiwaki 1959, 1962); (2) even the two outliers were longer than the minimum length for a pregnant female measured by Soviet whaling biologists (Tomilin 1967); and (3) the mean length of NAs did not differ significantly from maternal lengths.

The attraction of escorts to longer females may reflect several factors related to male reproductive success. One is that longer female size implies a greater likelihood of sexual maturity as was shown by the ogival fit to the relationship between female length and sexual maturity derived from the Japanese whaling data. When we applied this ogival function to our measured NA lengths, 26 (62%) of the 42 NAs we measured were of lengths with probability of sexual maturity of 0.5 or greater.



**Figure 7.** Scatter plot of the length of each calf versus the ordinal date of its measurement. The regression line fitting the data is shown together with the regression equation and the  $R^2$  value.



**Figure 8.** Scatter plot of the length of each mother versus the length of its calf. The regression line fitting the data is shown together with the regression equation and the  $R^2$  value.

A second factor is the likelihood that larger females will be more successful in rearing calves than will smaller females. Larger-sized individuals can store more energy reserves in the form of lipid-rich blubber than can smaller-sized individuals (Castellini 2002; Iverson 2002). This energy store is especially critical for a humpback mother that, although fasting during the several weeks to months of calf rearing in the winter breeding grounds (Craig et al. 2001), must sustain herself and her nursing calf by metabolizing the fat reserves accumulated during the previous summer/autumn season in high-latitude feeding areas. A larger body size not only allows for more fat storage but also for more effective energy conservation due to more efficient thermal regulation (the ratio of body surface area to body volume decreases with increasing body size; Castellini 2002; Iverson 2002). Additionally, longer females are likely to be older and thus more experienced in calf rearing than are smaller females (Clapham 2000). Calf mortality is high among humpback whales. Gabriele et al. (2001) estimated calf mortality at 18%, based on the number of females with calf photographically captured during the Hawaiian winter season and the number of those seen without calf in the subsequent summer feeding season in Alaskan waters. Thus, males choosing to mate with larger females should have an increased probability of fathering a calf that will survive through to its recruitment into the population.

In support of these ideas, we found that longer humpback whale mothers were associated with longer calves and that this relationship was not a function of the time of season that mother–calf pairs were measured. In particular, a multiple regression analysis showed that the positive relationship between mother length and calf length was still obtained even when ordinal date was held constant. The relatively low  $R^2$  value of 0.19 for the regression of mother length on calf length may be partly because, upon measurement, calf age was unknown. Consequently, it is probable that younger, small calves were measured for some large females and older, larger calves were measured for some small females. Nevertheless, the finding of a positive relationship between mother length and calf length despite this potentially confounding factor strengthens the argument that larger mother size results in larger calf size. That larger individuals can build up more stored energy reserves than can smaller individuals (Calder 1984) suggests that larger calves may be more fit and consequently will have a greater chance of survival than will smaller calves, as has been shown in other species (Clutton-Brock et al. 1988). Large calf size is especially important considering the long northbound migration (ca. 4000 km) to the high-latitude summer feeding grounds that calves departing Hawaii undertake in the company of their mothers.

A positive relationship between mother size and offspring size has been observed in other marine mammal species. Using aerial photogrammetry, Best & Ruther (1992) determined that primiparous female right whales (i.e. those photographed for the first time with a calf) were smaller and had smaller calves than did assumed multiparous females (i.e. those that were seen for the first time with a calf at least 5 years previously). Nernini et al. (1984) attributed the positive correlation between the size of bowhead whale, *Balaena mysticetus*, mothers and calves to larger females either giving birth earlier in the season or giving birth to larger calves. In California sea lions, *Zalophus californianus*, male and female pup mass gain was positively correlated with maternal mass (Ono & Boness 1996). The authors attributed this relationship to the ability of larger and older females to forage more efficiently during lactation rather than to greater use of energy reserves. From the existing data for humpback whales, it cannot be determined whether the increased calf size is present at birth and/or results from faster postpartum growth. Increased foraging efficiency during lactation is not responsible for increased calf size, because, as was noted, adult humpback whales do not feed during the winter months when calves are born (Chittleborough 1965; Dawbin 1966). However, a female's foraging efficiency prior to arrival on the breeding grounds can in theory affect a calf's size and/or growth. A more efficiently foraging female should be better able to accumulate greater energy stores (e.g. thicker blubber), and thus provide more nutrition to the calf both during the last stages of gestation and during lactation than can a less efficiently foraging female.

In theory, discrimination among potential mates by a male may be predicted whenever such discrimination is likely to affect that male's reproductive success (Fisher 1958) and where mating costs are involved (Dewsbury 1982). Thus, males should discriminate between females whenever mating opportunities are limited and females vary significantly in their reproductive potential and/or their ability to produce high-quality offspring (Berger 1989; Andersson 1994; Owens & Thompson 1994). In an earlier study, Craig et al. (2002) found that male humpback whales preferentially associate with female humpbacks without calf (i.e. those with a higher reproductive potential; Chittleborough 1958; Craig et al. 2002) than females with calf. Craig et al. (2002) proposed that discrimination among female humpbacks by males based on their reproductive potential might have been selected for because of the energetic and reproductive costs that males incur on the breeding grounds. These include loss of body mass over the season (Nishiwaki 1959), energy expended during competition (e.g. Baker & Herman 1984) and limits in spermatozoa production (see Chittleborough

1955). Our data on the positive relation between the length of the NA and the number of accompanying escorts suggest that male humpbacks may also express their choosiness by preferentially associating with larger (longer body length) females. We have shown that longer females are associated with longer calves, even when accounting for seasonal differences in calf length. We have argued that longer calves are likely to have greater survival probability than shorter calves (either because longer calves have longer mothers with greater nutritional reserves and/or because longer calves have greater body mass). Therefore in theory, a male that selectively mates with longer females should experience greater reproductive success than a male that mates indiscriminately among different-sized females.

Obviously, there is a cost to increased choosiness: it comes with increased competition. Game theory predicts that the cost that competitors are willing to accept increases as the value of the resource being competed for increases (Maynard Smith & Parker 1976; Parker & Rubenstein 1981). Given the risks of injury that male humpback whales face in competitive groups (e.g. Baker & Herman 1984; Pack et al. 1998; Herman et al. 2008) and the more general costs in terms of energy reserves expended when actively competing, our results suggest that males may be more willing to take such risks and incur such costs when females are larger.

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### References

- Andersson, M. 1994. *Sexual Selection*. Princeton, New Jersey: Princeton University Press.
- Baker, C. S. & Herman, L. M. 1984. Aggressive behavior between humpback whales (*Megaptera novaeangliae*) wintering in Hawaiian waters. *Canadian Journal of Zoology*, **62**, 1922–1937.
- Baker, C. S., Herman, L. M., Perry, A., Lawton, W. S., Straley, J. M., Wolman, A. A., Kaufman, G. D., Winn, H. E., Hall, J. D., Reinke, J. M. & Ostman, J. 1986. Migratory movement and population structure of humpback whales (*Megaptera novaeangliae*) in the central and eastern North Pacific. *Marine Ecology Progress Series*, **31**, 105–119.
- Baker, C. S., Perry, A. & Herman, L. M. 1987. Reproductive histories of female humpback whales *Megaptera novaeangliae* in the North Pacific. *Marine Ecology Progress Series*, **41**, 103–114.
- Barlow, J. & Clapham, P. J. 1997. A new birth-interval approach to estimating demographic parameters of humpback whales. *Ecology*, **78**, 535–546.
- Berger, J. 1989. Female reproductive potential and its apparent evaluation by male mammals. *Journal of Mammalogy*, **70**, 347–358.
- Best, P. B. & Ruther, H. 1992. Aerial photogrammetry of southern right whales, *Eubalaena australis*. *Journal of Zoology*, **228**, 595–614.
- Brown, M. R., Corkeron, P. J., Hale, P. T., Schultz, K. W. & Bryden, M. M. 1995. Evidence for a sex segregated migration in the humpback whale (*Megaptera novaeangliae*). *Proceedings of the Royal Society of London, Series B*, **259**, 229–234.
- Brownell, R. Jr. & Ralls, K. 1986. Potential for sperm competition in baleen whales. *Reports of the International Whaling Commission, Special Issue*, **8**, 97–112.
- Caldar, W. A. 1984. *Size, Function, and Life History*. Cambridge, Massachusetts: Harvard University Press.
- Castellini, M. 2002. Thermoregulation. In: *Encyclopedia of Marine Mammals* (Ed. by W. F. Perrin, B. Würsig, C. M. Thewissen & C. R. Crumley), pp. 1245–1250. New York: Academic Press.
- Chittleborough, R. G. 1955. Aspects of reproduction in the male humpback whale, *Megaptera nodosa* (Bonnatere). *Australian Journal of Marine and Freshwater Research*, **6**, 1–29.
- Chittleborough, R. G. 1958. The breeding cycle of the female humpback whale, *Megaptera nodosa* (Bonnatere). *Australian Journal of Marine and Freshwater Research*, **9**, 1–18.
- Chittleborough, R. G. 1965. Dynamics of two populations of the humpback whale, *Megaptera novaeangliae* (Borowski). *Australian Journal of Marine and Freshwater Research*, **16**, 33–128.
- Clapham, P. J. 1992. The attainment of sexual maturity in humpback whales. *Canadian Journal of Zoology*, **70**, 1470–1472.
- Clapham, P. J. 1996. The social and reproductive biology of humpback whales: an ecological perspective. *Mammal Review*, **26**, 27–49.
- Clapham, P. J. 2000. The humpback whale: seasonal feeding and breeding in a baleen whale. In: *Cetacean Societies: Field Studies of Dolphins and Whales* (Ed. by J. Mann, R. C. Connor, P. L. Tyack & H. Whitehead), pp. 173–196. Chicago: University of Chicago Press.
- Clapham, P. J., Palsboll, P. J., Mattila, D. K. & Vasquez, O. 1992. Composition and dynamics of humpback whale competitive groups in the West Indies. *Behaviour*, **122**, 182–194.
- Clapham, P. J., Wetmore, S. E., Smith, T. D. & Mead, J. C. 1999. Length at birth and at independence in humpback whales. *Journal of Cetacean Management*, **1**, 141–146.
- Clutton-Brock, T. H., Albon, S. D. & Guinness, F. W. 1988. Reproductive success in male and female red deer. In: *Reproductive Success* (Ed. by T. H. Clutton-Brock), pp. 325–343. Chicago: University of Chicago Press.
- Craig, A. S. & Herman, L. M. 1997. Sex differences in site fidelity and migration of humpback whales (*Megaptera novaeangliae*) to the Hawaiian Islands. *Canadian Journal of Zoology*, **75**, 1923–1933.
- Craig, A. S., Herman, L. M. & Pack, A. A. 2001. *Estimating Residence Times of Humpback Whales in Hawaii. Report to the Hawaiian Islands Humpback Whale National Marine Sanctuary Off of National Marine Sanctuaries, National Oceanic and Atmospheric Administration*. Honolulu: U.S. Department of Commerce and Department of Land and Natural Resources.
- Craig, A. S., Herman, L. M. & Pack, A. A. 2002. Male mate choice and male–male competition coexist in the humpback whale (*Megaptera novaeangliae*). *Canadian Journal of Zoology*, **80**, 745–755.
- Craig, A. S., Herman, L. M., Gabriele, C. M. & Pack, A. A. 2003. Migratory timing of humpback whales (*Megaptera novaeangliae*) in the central North Pacific varies with age, sex and reproductive status. *Behaviour*, **140**, 981–1001.
- Dawbin, W. H. 1966. The seasonal migratory cycle of humpback whales. In: *Whales, Dolphins and Porpoises* (Ed. by K. S. Norris), pp. 145–170. Berkeley: University of California Press.
- Dewsbury, D. A. 1982. Ejaculate cost and male choice. *American Naturalist*, **119**, 601–610.
- Downhower, J. F. & Brown, L. 1981. The timing of reproduction and its behavioral consequences for mottled sculpins, *Cottus bairdi*. In: *Natural Selection and Social Behavior* (Ed. by R. D. Alexander & D. W. Tinkle), pp. 78–95. New York: Chiron Press.
- Fedak, M. A., Wilson, B. & Pomeroy, P. P. 2002. Reproductive behavior. In: *Encyclopedia of Marine Mammals* (Ed. by W. F. Perrin, B. Würsig, C. M. Thewissen & C. R. Crumley), pp. 1015–1027. New York: Academic Press.
- Fisher, R. A. 1958. *The Genetical Theory of Natural Selection*, 2nd edn. New York: Dover.
- Gabriele, C. M., Straley, J. M., Mizroch, S. A., Baker, C. S., Craig, A. S., Herman, L. M., Glockner-Ferrari, D., Ferrari, M. J., Cerchio, S., von Ziegesar, O., Darling, J., McSweeney, D., Quinn T. J. II, & Jacobsen, J. K. 2001. Estimating the mortality rate of humpback whale calves in the central North Pacific Ocean. *Canadian Journal of Zoology*, **79**, 589–600.
- Glockner, D. A. 1983. Determining the sex of humpback whales (*Megaptera novaeangliae*) in their natural environment. In: *Communication and Behavior of Whales* (Ed. by R. Payne), pp. 447–464. Boulder: Westview Press.
- Herman, E. Y. K., Herman, L. M., Pack, A. A., Marshall, G., Shepard, C. M. & Bakhtiari, M. 2008. When whales collide: Crittercam offers insights into the competitive behavior of humpback whales on their Hawaiian wintering grounds. *Marine Technology Society Journal*, **41**, 35–43.
- Herman, L. M. & Antinova, R. C. 1977. Humpback whales in the Hawaiian breeding waters: population and pod characteristics. *Scientific Reports of the Whales Research Institute*, **29**, 59–85.
- Herman, L. M. & Tavalga, W. N. 1980. The communication systems of cetaceans. In: *Cetacean Behavior: Mechanisms and Functions* (Ed. by L. M. Herman), pp. 149–209. New York: Wiley Interscience.
- Herman, L. M., Forestell, P. H. & Antinova, R. C. 1980. *Study of the 1976/77 Migration of Humpback Whales into Hawaiian Waters: Composite Description. Final Report to the U.S. Marine Mammal Commission (Report No. MMC-77/19)*. Arlington, Virginia: United States National Technical Information Services.
- Iverson, S. J. 2002. Blubber. In: *Encyclopedia of Marine Mammals* (Ed. by W. F. Perrin, B. Würsig, C. M. Thewissen & C. R. Crumley), pp. 107–112. New York: Academic Press.

- Katona, S., Baxter, B., Brazier, O., Kraus, S., Perkins, J. & Whitehead, H.** 1979. Identification of humpback whales by fluke photographs. In: *Behavior of Marine Animals: Current Perspectives in Research*. Vol. 3. *Cetaceans* (Ed. by H. E. Winn & B. L. Olla), pp. 33–44. New York: Plenum.
- Katona, S. K. & Beard, J. A.** 1990. Population size, migrations and feeding aggregations of the humpback whale (*Megaptera novaeangliae*) in the western North Atlantic Ocean. *Reports of the International Whaling Commission, Special Issue*, **12**, 295–305.
- Maynard Smith, J. & Parker, G. A.** 1976. The logic of asymmetric contests. *Animal Behaviour*, **24**, 159–175.
- Mobley, J. R. & Herman, L. M.** 1985. Transience of social affiliations among humpback whales (*Megaptera novaeangliae*) on the Hawaiian wintering grounds. *Canadian Journal of Zoology*, **63**, 762–772.
- Mobley, J. R., Bauer, G. B. & Herman, L. M.** 1999. Changes over a ten-year interval in the distribution and relative abundance of humpback whales (*Megaptera novaeangliae*) wintering in Hawaii. *Aquatic Mammals*, **25**, 63–72.
- Nernini, M. K., Braham, H. W., Marquette, W. M. & Rugh, D. J.** 1984. Life history of the bowhead whale, *Balaena mysticetus* (Mammalia: Cetacea). *Journal of Zoology*, **204**, 443–468.
- Nishiwaki, M.** 1959. Humpback whales in Ryukyuan waters. *Scientific Reports of the Whales Research Institute*, **12**, 49–87.
- Nishiwaki, M.** 1962. Ryukyuan whaling in 1961. *Scientific Reports of the Whales Research Institute*, **16**, 19–28.
- Omura, H.** 1955. Whales in the northern part of the North Pacific. *Norsk Hvalfangst-Tidende*, **7**, 395–405.
- Ono, K. A. & Boness, D. J.** 1996. Sexual dimorphism in sea lion pups: differential maternal investment, or sex-specific differences in energy allocation? *Behavioral Ecology and Sociobiology*, **38**, 31–41.
- Owens, I. P. F. & Thompson, D. B. A.** 1994. Sex differences, sex ratios and sex roles. *Proceedings of the Royal Society of London, Series B*, **258**, 93–99.
- Pack, A. A., Salden, D. R., Ferrari, M., Glockner-Ferrari, D., Herman, L. M., Stubbs, H. A. & Straley, J. M.** 1998. Male humpback whale dies in competitive group in Hawaii. *Marine Mammal Science*, **14**, 861–873.
- Pack, A. A., Herman, L. M., Craig, A. S., Spitz, S. S. & Deakos, M. H.** 2002. Penis extrusions by humpback whales (*Megaptera novaeangliae*). *Aquatic Mammals*, **28**, 131–146.
- Parker, G. A. & Rubenstein, D. I.** 1981. Role assessment, reserve strategy, and acquisition of information in asymmetric animal conflicts. *Animal Behaviour*, **29**, 221–240.
- Perry, A., Mobley, J. R. Jr, Baker, C. S. & Herman, L. M.** 1988. *Humpback Whales of the Central and Eastern North Pacific: a Catalog of Individual Identification Photographs* Honolulu, Hawaii: Sea Grant Miscellaneous Reports, UNIH-SEA GRANT-NR-88-02.
- Preston, B. T., Stevenson, I. R., Pemberton, J. M., Coltman, D. W. & Wilson, K.** 2005. Male mate choice influences female promiscuity in Soay sheep. *Proceedings of the Royal Society of London, Series B*, **272**, 365–373.
- Ralls, K.** 1976. Mammals in which females are larger than males. *Quarterly Review of Biology*, **51**, 245–276.
- Ralls, K. & Mesnick, S. L.** 2002. Sexual dimorphism. In: *Encyclopedia of Marine Mammals* (Ed. by W. F. Perrin, B. Wursig, C. M. Thewissen & C. R. Crumley), pp. 1071–1078. New York: Academic Press.
- Rowland, W. J.** 1982. Mate choice by male sticklebacks, *Gasterosteus aculeatus*. *Animal Behaviour*, **30**, 1093–1098.
- Sargent, R. C., Gross, M. R. & Van Den Berghe, E. P.** 1986. Male mate choice in fishes. *Animal Behaviour*, **34**, 545–550.
- Shine, R., Webb, J. K., Lane, A. & Mason, R. T.** 2006. Flexible mate choice: a male snake's preference for larger females is modified by the sizes of females encountered. *Animal Behaviour*, **71**, 203–209.
- Spitz, S. S., Herman, L. M. & Pack, A. A.** 2000. Measuring sizes of humpback whales (*Megaptera novaeangliae*) through underwater videogrammetry. *Marine Mammal Science*, **16**, 664–676.
- Spitz, S. S., Herman, L. M., Pack, A. A. & Deakos, M. H.** 2002. The relation of body size of male humpback whales to their social roles on the Hawaiian winter grounds. *Canadian Journal of Zoology*, **80**, 1938–1947.
- Tomilin, A. G.** 1967. *Mammals of the U.S.S.R. and Adjacent Countries*. Vol. IX. *Cetacea*. Jerusalem: Israel Program for Scientific Translations.
- True, F. W.** 1904. The whalebone whales of the western North Atlantic compared with those occurring in European waters; with some observations on the species of the North Pacific. *Smithsonian Contributions to Knowledge*, **33**, 1–318.
- Tyack, P. & Whitehead, H.** 1983. Male competition in larger groups of wintering humpback whales. *Behaviour*, **83**, 132–154.