The relation of body size of male humpback whales to their social roles on the Hawaiian winter grounds

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Abstract: We examined the relation of body length of male humpback whales (*Megaptera novaeangliae*) to the social roles they adopted on the Hawaiian winter grounds: principal escort in a competitive group, secondary escort, lone escort to a mother–calf pair, male partner in a dyad, and singer. Using underwater videogrammetry, we measured body lengths of 17 principal escorts, 68 secondary escorts, 40 single escorts, 17 male partners, and 8 singers. Results revealed that (*i*) principal escorts were, on average, significantly larger than males in each of the remaining social roles except singer, (*ii*) singers were significantly larger than male partners, (*iii*) there were no significant size differences among secondary escorts, single escorts, or male partners. Further, principal escorts tended to be the largest or second-largest male within their individual competitive group. All principal escorts were of sizes that indicated a 0.81 probability or better of sexual maturity, based on whaling data. In comparison, more than half of the male partners, almost one-third of the secondary escorts, and one-fifth of the single escorts were of sizes that indicated a 0.5 probability or less of sexual maturity. Seven of the eight singers had a 0.9 probability or better of sexual maturity and the eighth singer a 0.5 probability. However, the data for singers are too few to allow firm conclusions to be reached about the relation of body size to singing. Overall, our findings suggest that body size confers an advantage in physical competition between male humpback whales, and that a large proportion of males adopting the role of secondary escort, single escort, and partner are likely to be sexually immature. Additionally, the competitive group appears to be a major reproductive unit in terms of bringing together a receptive female and potential mates.

Résumé : Nous avons examiné, chez des mâles de la baleine à bosse (*Megaptera novaeangliae*), la relation entre la longueur du corps et la fonction sociale qu'ils assument dans leurs quartiers d'hiver à Hawai'i : escorte principale dans un groupe compétitif, escorte secondaire, seule escorte d'un groupe mère–petit, partenaire mâle dans une dyade et chanteur. La vidéogrammométrie sous-marine nous a permis de mesurer la longueur du corps de 17 escortes principales, 68 escortes secondaires, 40 escortes seules, 17 partenaires mâles et 8 chanteurs. Les résultats ont révélé (*i*) que les escortes principales étaient de longueur significativement supérieure à celle des mâles des autres groupes sociaux, à l'exception des chanteurs, (*ii*) que les chanteurs étaient de taille significativement plus élevée que les mâles partenaires et (*iii*) qu'il n'y avait pas de différence significative de taille entre les escortes secondaires, les escortes seules et les mâles partenaires. De plus, le escortes principales avaient tendance à être les mâles les plus gros ou les deuxièmes plus gros au sein de leurs groupes compétitifs respectifs. Toutes les escortes principales avaient une taille reliée à une probabilité de 0,81 ou plus d'être à maturité sexuelle d'après les données de chasse à la baleine. Par comparaison, plus de la moitié des mâles partenaires, près d'un tiers des escortes secondaires et un cinquième des escortes seules étaient de taille associée à une probabilité de 0,5 ou moins d'être à maturité sexuelle. Sept des huit mâles chanteurs avaient une taille associée à une probabilité de 0,9 ou plus d'être à maturité sexuelle et le huitième, une probabilité de 0,5. Cependant, les données sur les chanteurs sont trop peu nombreuses pour qu'on puisse tirer des conclusions sur la relation entre la taille et le chant. Dans l'ensemble, nos données indiquent que la taille confère un avantage dans la compétition physique entre les baleines à bosse mâles et qu'une importante proportion des escortes secondaires, des mâles seuls et des mâles partenaires sont probablement immatures. En outre, les groupes compétitifs semblent être des unités reproductives majeures en ce qu'ils favorisent la rencontre d'une femelle réceptive avec des partenaires potentiels.

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Introduction

Body size is a reliable predictor of intraspecific competitive ability and reproductive success in a wide variety of taxa, including gall aphids (*Pemphigus* spp.; Whitham 1979), common toad (*Bufo bufo*; Davies and Halliday 1978), marine iguanas (*Amblyrhynchus cristatus*; Wikelski et al. 1996), red deer (*Cervus elaphus*; Clutton-Brock et al. 1982), elephant seals (*Mirounga* spp.; Le Boeuf 1974; Modig 1996), and African elephant (*Loxodonta africana*; Poole 1989). Animals may adopt different social roles or behavioral strategies as a function of their body size relative to other members of their species. For example, large bull elephant seals are more successful than are smaller males at defending and maintaining groups of females and in challenging bulls guarding female groups (Le Boeuf 1974; Modig 1996). Smaller bulls engage in challenges less frequently and adopt a "satellite" strategy by remaining on the perimeter of groups of females guarded by a large bull, waiting for opportunities to "sneak" copulations while the resident bull is otherwise occupied. In this system, the largest males mate the most frequently. Similarly, only the largest male marine iguanas can defend territories within a lek mating system (Wikelski et al. 1996). Smaller males remain outside the boundaries of the territories and some may simulate female iguanas to gain proximity to females.

In this paper we present data on measured lengths of male humpback whales (*Megaptera novaeangliae*) occupying various social roles during the annual winter assembly of humpback whales in Hawaiian waters, the principal wintering grounds for North Pacific humpback whales.

While on their winter grounds, humpback whales do not feed (Chittleborough 1965; Dawbin 1966), so social relations are not determined by prey resources. Instead, increases in gonad size and spermatogenesis in males and ovulatory activity in females during the fall and winter season suggest that much of the behavior observed on the winter grounds is directed toward mating (Chittleborough 1954, 1955*a*, 1955*b*; Symons and Weston 1958; Nishiwaki 1959). The different social roles that male humpbacks may occupy on the winter grounds can be labeled escort, singer, or partner (Herman and Antinoja 1977; Tyack 1981; Glockner 1983; Tyack and Whitehead 1983; also personal observations). The roles of singer and escort may be further differentiated, as described later. It seems probable that body size is a significant factor in the social roles adopted by male humpback whales and in their success in those roles. However, there are no published data on the relation of body size to these various social roles. To measure the length of whales, we used the underwater videogrammetric technique described by Spitz et al. (2000), who showed that this technique is accurate and reliable. An advantage of the technique, compared with aerial photogrammetry, is that the snorkeler can often identify the sex of the targeted whale as well as that of other whales in a group by observing the presence (in females) or the absence (in males) of the hemispheric lobe just caudal to the genital slit (e.g., see Glockner 1983). Further, the snorkeler's underwater observations, together with surface observations made from the boat and the video record obtained, can reveal behavior patterns and social roles of the animals.

Herman and Antinoja (1977) first described an "escort" as a whale (or whales) accompanying a mother–calf pair. Subsequent studies verified the gender of escorts accompanying a female either with or without a calf as male (e.g., Glockner 1983; Clapham et al. 1992). A striking feature of humpback whale behavior on the winter grounds, seen from time to time, is physical competition among escorts for the female, in groups that range in size from 2 to as many as 15 or more escorts (Tyack and Whitehead 1983; Baker and Herman 1984; Mattila et al. 1989; Clapham et al. 1992). Typically, males in these competitive groups engage in agonistic behaviors, using threat displays and body contact to vie for proximity to the single female in the group (Tyack and Whitehead 1983; Baker and Herman 1984). The male closest to the female is termed the principal escort and the other males are termed secondary escorts (Tyack and Whitehead 1983). The intensity of aggression among the escorts can at times escalate to physical injury (Darling et al. 1983; Baker and Herman 1984; Mattila et al. 1989; Pack et al. 1998). Males clearly expend considerable energy during these encounters. For the lone female, the competitive group may function in part as a selection mechanism allowing her to evaluate male fitness and thereby exercise some choice among potential mates. Defense of multiple females by males is not an option, inasmuch as female humpbacks are, on average, somewhat larger than males (e.g., Tomilin 1967), the operational sex ratio in the winter waters appears to be on the order of two males to one female, and adult females on the winter grounds are rarely found together (Herman and Tavolga 1980; Mattila et al. 1989; Clapham et al. 1992; Brown and Corkeron 1995; Craig and Herman 1997; Smith et al. 1999).

Using data obtained by means of the videogrammetric technique, we provide comparisons between the lengths of principal and secondary escorts to test for a relationship between body size and success in physical competition. If body size is important to success in physical competition among humpback whales, then one would expect to find that principal escorts were, on average, larger than secondary escorts.

In addition to these competitive groups, it is common to see a single escort accompanying a mother–calf pair. How does the size of escorts in that role compare with the size of those in competitive groups? If escorts are seeking mating opportunities (actual mating in humpback whales has never been observed; e.g., see Herman and Tavolga 1980; Clapham 2000; Pack et al. 2002), then males might be expected to seek out females having the highest reproductive potential. Adult female humpback whales produce one calf every 2–3 years, on average (Mackintosh 1942; Chittleborough 1958; Baker et al. 1987; Barlow and Clapham 1997). Although annual reproduction has been reported occasionally (Glockner-Ferrari and Ferrari 1984; Baker et al. 1987; Weinrich et al. 1993; Straley et al. 1994), postpartum estrus is relatively rare (Chittleborough 1955*b*). Of the 19 lactating females examined by Chittleborough (1958), 8 (42%) were also pregnant, compared with 67 of 75 (89.3%) nonlactating females. In addition, Craig et al. (2002) reported that female humpback whales observed on the winter grounds without a calf were more likely to be found with a calf than without a calf the following year. Conversely, females sighted with a calf were more likely to be sighted without a calf than with a calf the following year. These findings support earlier whaling

data on the greater reproductive potential of females without a calf than of females with a calf. Consequently, it might be expected that larger males would preferentially associate with sexually mature females without a calf, and that smaller males, presumably less capable competitively, would be found more commonly in association with mother–calf pairs. To test this hypothesis, we compare average sizes of lone escorts in association with a mother–calf pair with the average sizes of principal and secondary escorts in competitive groups.

The humpback whale winter grounds are characterized by contemporaneous singing by multiple males. This behavior seems somehow related to reproduction, but its exact function is still in question (Baker and Herman 1984; Chu and Harcourt 1986; Chu 1988; Helweg et al. 1992; Frankel et al. 1995; Clapham 1996; Frazier and Mercado 2000; Darling and Bérubé 2001). What role does body size play in singing? Are singers a random sample of males, or are they more closely related in size to males in one of the escort roles? Singers do assume the role of escort (and vice versa) (e.g., Tyack 1981), and occasionally, escorts will sing while accompanying a mother–calf pair (Herman and Tavolga 1980; Baker and Herman 1984; Frankel et al. 1995; Darling and Bérubé 2001). Most commonly, however, singers are lone animals that remain relatively stationary in the water column at depths of perhaps 15–25 m. Comparisons of the size of singers with the sizes of males in other social roles can help clarify who the singers are and how singing may interface with the humpback whale mating system.

A final male social grouping considered in this paper is the dyad. Whales in a dyad of two adults without a calf are termed partners and are common on the winter grounds. The composition of the dyad may be two males or a male and female. As noted earlier, adult females rarely associate with each other on the winter grounds. Should we consider a dyad consisting of a male–female pair to be simply another form of escorting, or is the association more typically identified with smaller, possibly sexually immature whales? To help answer this question we compare the sizes of males in dyads with the sizes of males occupying other social roles.

Finally, to classify the sexual maturity of sized whales, we use data on the sizes of sexually mature male North Pacific humpback whales obtained by whaling biologists, mainly during the first six decades of the 20th century. These data are available in several sources (e.g., Omura 1955; Nishiwaki 1959, 1962; Slijper 1962; Rice 1963; Tomilin 1967).

Methods

Study area and dates

Observations of humpback whales were carried out in the waters of the "four-island region" between the islands of Maui, Lanai, Kahoolawe, and Molokai from February to April of 1997 and from January to April of 1998 and 1999. The waters of the four-island region (consisting of the Auau, Kalohi, and Pailolo channels) contain one of the densest concentrations of humpback whales in the Hawaiian Island chain during the winter season (e.g., Herman et al. 1980; Mobley et al. 1999).

Observation methods

We approached humpback whales daily, using small (5.2–6.0 m) outboard-engine boats. Typically, our observation effort continued throughout the day from approximately 08:30 to 17:00, weather and sea state permitting. Most of our effort was in the lee areas between west Maui and north Lanai Island, comprising approximately 340 km^2.

Single whales or groups of whales sighted by observers aboard the vessels were approached for close study (under Federal and State research permits), without bias toward any particular type of group. During the approach, general behavior patterns were identified and recorded. To the extent possible, identification photographs of the underside of the tail flukes (Katona et al. 1979) were obtained using 35-mm cameras equipped with 300-mm lenses, and the observed social roles of the photographed whales were manually recorded. Generally, a single whale or group of whales was tracked until all or almost all individuals had been identified photographically, the social category of the group established (e.g., competitive group, mother–calf escort, dyad), and the social roles of individual animals determined (e.g., principal escort, secondary escort). The length of observation for a group typically ranged from 30 to 60 min but could be as long as several hours. Singers were identified by the presence of loud song and by the apparent attenuation of the song as the focal whale surfaced (Tyack 1983). Singers could usually be seen as well as heard by a researcher snorkeling at the surface. Most often, the singer was stationary and canted head downward at about a 30–60° angle.

If the whales under observation were stationary, milling, or slowly moving, we deployed a swimmer equipped with mask, snorkel, and fins and carrying a high-frequency (200 kHz) sonar device (Speedtech Depthmate) and a digital video camera (Sony DCR-TRV-7) in an underwater Jay-Mar VM-6000 housing. The goals of the swimmer were to obtain video records of the whales suitable for subsequent size analyses, to make underwater visual and video records of behavior and social interactions, and to determine the sex of individual whales by the presence (in females) or absence (in males) of a hemispheric lobe at the caudal termination of the genital slit (see True 1904; Glockner 1983).

Full details of the videogrammetric technique are available in Spitz et al. (2000). In brief, to gather videogrammetric data the swimmer made a continuous video record of the whale. Distance to the whale was measured with the sonar device when the whale was perpendicular to the longitudinal axis of the camera and underwater visibility was sufficient to allow identification of the anterior and posterior ends of the whale. Multiple independent measurements were obtained as the videographer moved relative to a stationary whale, when the whale moved and the videographer repositioned himself or herself, or when the whale swam off and then slowed down again, presenting another opportunity for the boat to approach and deploy the swimmer. Any or all of these conditions might occur with a given whale. Our goal was 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. (2000) demonstrated that for whales occupying a given social role, there was no significant difference between the mean lengths of those for which there were two independent measures and

Table 1. Length measurements for male humpback whales (*Megaptera novaeangliae*) occupying the indicated social roles when measured.

			Length (m)				
Social role	No. of independent measures	No. of whales	Mean	Median	SD	Range	Mean CV
Principal escort	1	7	12.40	12.01	0.897	11.66–14.03	na
	2	5	12.53	12.45	0.543	11.88–13.39	2.11
	3 or more	5	12.29	12.20	0.622	11.76–13.34	2.67
Total		17	12.41	12.22	0.694	11.66–14.03	2.39
Secondary escort	1	50	11.58	11.61	0.832	9.95–13.11	na
	2	10	11.51	11.56	1.285	9.03–13.15	3.13
	3 or more	8	12.17	12.01	0.511	11.42–12.83	3.74
Total		68	11.64	11.71	0.891	9.03–13.15	3.40
Single escort	1	21	11.70	11.69	0.756	10.40–13.51	na
	2	9	11.91	11.91	0.367	11.25–12.44	2.28
	3 or more	10	11.63	11.61	0.243	11.27–12.02	2.74
Total		40	11.73	11.69	0.587	10.40–13.51	2.52
Singer	1	6	12.08	12.06	0.506	11.29–12.85	na
	2	2	12.06	12.06	0.042	12.03–12.09	0.03
	3 or more	0	na	na	na	na	na
Total		8	12.08	12.06	0.428	11.29–12.85	0.03
Male partner	1	3	11.38	11.11	1.330	10.20–12.82	na
	2	6	11.80	11.85	0.847	10.58–12.69	3.93
	3 or more	8	11.02	11.30	0.997	9.33–12.06	2.71
Total		17	11.36	11.32	1.005	9.33–12.82	3.24

Note: The number of independent measures refers to the number of unique videogrammetric "captures" made of the targeted whale at the time of measurement (see the text); na, not applicable.

the mean lengths of those for which there were three or more independent measures. Singers were videotaped during the portion of their ascent or descent when they were horizontal or nearly so. Videotaping a singer that was at depth and canted head downward produced foreshortening and was therefore not a suitable "capture" for length measurements. The requirement to wait until the whale began to surface or submerge restricted opportunities for obtaining measurements of singers, however.

Data analyses

Subsequent to fieldwork, digital video images of whales recorded concurrently with sonar distance measurements were captured on a personal computer. The best images were measured using Adobe Photoshop software, employing basic photogrammetric principles as described in Spitz et al. (2000). For each whale measured, the mean of the independent measurements for that individual represented the whale's final measured length.

Results

Altogether, 150 male humpback whales were measured using the videogrammetric technique. Table 1 shows the mean lengths of these males as a function of their social role at the time of measurement. The data in Table 1 are organized by the number of independent measures of size obtained 1, 2, or 3 or more times. Each of the whales measured within each social role represented a unique individual, based on available fluke photographic identification. The mean coefficient of variation (CV) shown in Table 1 is the mean of the means of individual CVs for animals measured independently more than once during the same encounter in a day. The means of the CVs are uniformly low, attesting to the reliability of the videogrammetric procedure. To test the validity of including whales measured only once, for the 31 whales measured 3 or more times we compared the mean for the first measurement alone (11.75 m, SD = 0.887 m) with the mean for the first and second measurements combined (11.73 m, SD = 0.781 m) and with the mean for all available measurements combined (11.72 m, SD = 0.776 m). A general linear model repeated measures analysis of length revealed no significant difference among these mean lengths ($F_{[3,31]} = 0.101$, $p = 0.90$). Thus, the videogrammetric technique is useful even when opportunities for multiple independent measurements of a whale are limited.

As a further test of the reliability of the videogrammetric measurements, we examined our fluke-identification photographs to determine whether any of the 150 individual whales were measured on different days (i.e., if they represented a "recapture"). As shown in Table 2, two whales were measured twice in 1999, 2 and 10 days apart, and one whale was measured in 1998 and again in 1999, approximately 1 year and 18 days apart. The length differences were 0.01 and 0.09 m for the two whales measured in the same year and 0.21 m for the whale measured in successive years. In these three cases, the total of all length measurements obtained was used to compute the mean final length, and these whales were entered only once into Table 1. This was possible because the social role did not change from the first to the sec-

Table 2. Length measurements of three escort whales, each seen on two different dates as the sole escort to a mother–calf pair.

Date	Pod composition*	No. of independent measures	Measured length (m)	Length difference (m)	Length difference (%)	Final length (m)
1998-02-20	McE	1	11.74	0.21	1.76	11.92
1999-03-11	McE	7	11.95			
1999-01-23	McE	4	11.64	0.01	0.09	11.64
1999-01-25	McE	3	11.65			
1999-02-02	McE	2	11.48	0.09	0.78	11.52
1999-02-12	McE	2	11.57			

Note: The final length is the mean of all measurements for that whale, and the percent difference is the length difference as a percentage of the final length.
*M, mother; c, calf; E, escort.

ond measurement; all three whales were seen each time in the role of single escort to a mother–calf pair.

A comparison of mean lengths ("total") across the five social roles in Table 1 yielded an overall significant difference ($F_{[4,145]} = 4.63$, $p = 0.002$). Pairwise comparisons among the different social roles revealed that principal escorts were significantly larger than whales in all other categories except singer, and singers were significantly larger than male partners (Student–Newman–Keuls test, $p < 0.05$). No other pairwise comparisons were significant. These data support the hypothesis that the role of principal escort will tend to be occupied by larger males, presumably because larger size confers an advantage in physical competition.

The size differences between males occupying the various social roles are illustrated explicitly in Fig. 1, which shows the distribution of the mean measured sizes of individual whales within each social role (if a whale was measured only once, that measurement is used). It is apparent that the distribution of sizes is sharply attenuated at the lower end for principal escorts and somewhat so for singers, whereas all other social categories range more deeply into the smaller sizes.

Figure 2 presents the sizes at which male North Pacific humpbacks attain physical maturity, based on examinations of the carcasses of male North Pacific humpback whales: 109 by Nishiwaki (1959), 31 by Nishiwaki (1962), and 74 in two different whaling grounds by Omura (1955). The data points in Fig. 2 are based on all data combined for sizes from 10.67 m (35 ft) to 12.5 m (41 ft). All whales 10.67 m in length or smaller were found to be sexually immature and all whales 12.5 m or longer were found to be sexually mature. We have made an empirical fit to the data, using the cumulative normal probability density function

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

where = 11.26 and $\sigma = 0.47$. Using this function, the probability values of sexual maturity corresponding to different sizes are scaled on the lower horizontal axis, from 0.1 to 0.9. Thus, a male 10.7 m in length has a probability of sexual maturity of 0.1; the probability value increases to 0.3 at 11.0 m, 0.5 at 11.3 m, 0.7 at 11.5 m, and 0.9 at 11.9 m. These probability values versus size for North Pacific humpback whales are actually very similar to those calculated by

Fig. 1. The distribution of lengths of male humpback whales (*Megaptera novaeangliae*) occupying each of five social roles. Each shaded bar represents the mean size for the distribution. The two arrows facing each other show the location of the median. The horizontal lines bound the lengths of whales having a 0.5 probability (11.3 m) and a 0.9 probability (11.9 m) of being sexually mature, based on measurements of North Pacific male humpback whales by whaling biologists (see the text).

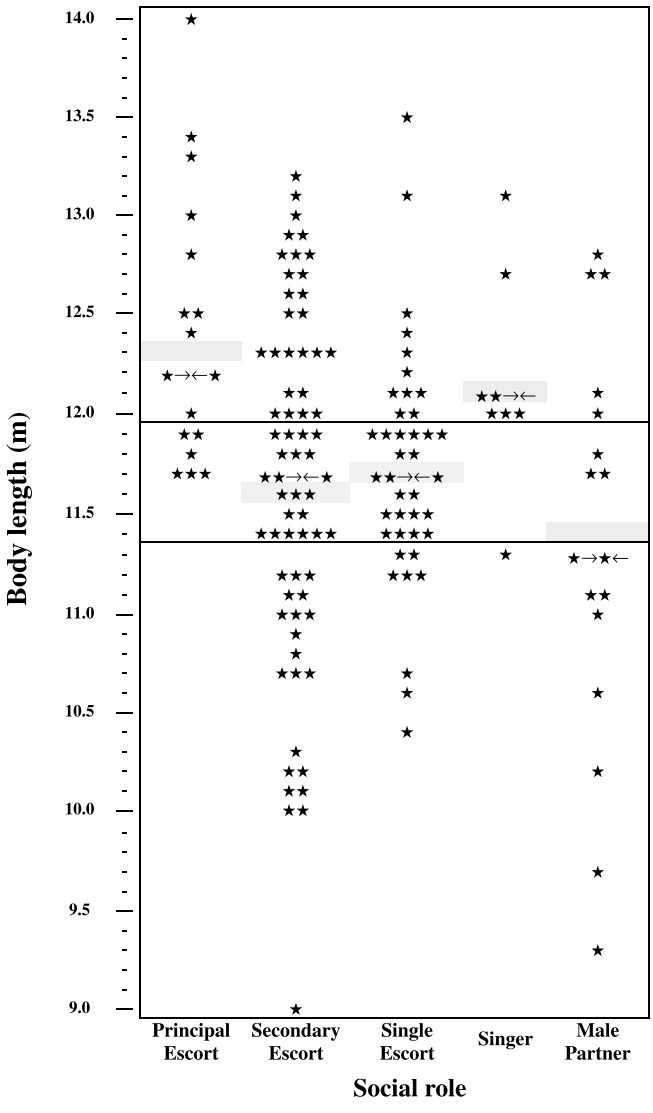
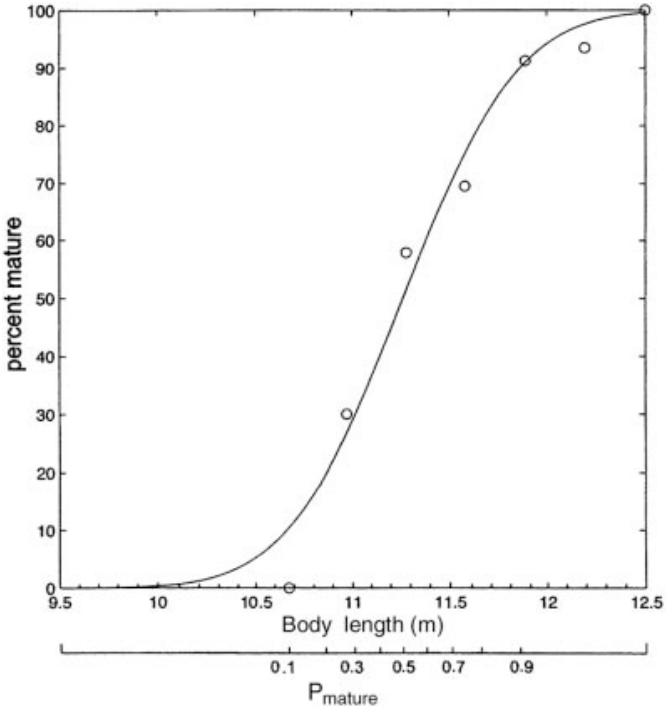


Fig. 2. Percentages of sexually mature North Pacific humpback whales as a function of body length, based on measurements of North Pacific male humpback whales by whaling biologists. The upper *x* axis shows length and the lower *x* axis shows the probability of sexual maturity, P_{mature}, associated with the different lengths, extrapolated from the sigmoid function (cumulative normal probability density function) fitted to the data points. The data points are taken from measurements provided by whaling biologists (see the text).



Chittleborough (1955*a*; Fig. 2) for 609 southern hemisphere male humpback whales caught from Western Australia shore stations between 1951 and 1953, a population different from the northern hemisphere whales studied by Nishiwaki and Omura.

Shown in Fig. 1, then, in addition to the number of whales of each size measured, are horizontal lines corresponding to probabilities of sexual maturity of 0.5 (11.3 m) and 0.9 (11.9 m). Figure 1 reveals that all principal escorts were longer than 11.6 m and more than three-fourths (76.5%) were 11.9 m or longer. The largest animal measured, at 14.03 m, was a principal escort. In contrast, only 36 (52.9%) of the 68 secondary escorts were longer than 11.6 m, 44.1% were 11.9 m or longer, and 30.9% were shorter than 11.3 m and hence likely to be sexually immature. One secondary escort may have been a yearling, as it measured only 9.03 m, and several others appeared to be of juvenile size (e.g., see Clapham et al. 1999).

A more compelling test of the size differences between principal and secondary escorts in competitive groups can be made by comparing sizes *within* each competitive group. Tables 3 and 4 list sizes of the principal escort (P) and secondary escorts (S) within each of 12 competitive groups for which measurements of the principal escort and at least some of the secondary escorts were obtained. Nine of these groups consisted of multiple males accompanying a female without a calf (the "nuclear animal", NA), and three consisted of multiple males accompanying a female with a calf (Mc). The numbers of escorts obtained from surface observations are listed (e.g., NA7E means that seven escorts were observed accompanying the nuclear animal and Mc3E means that three escorts were accompanying the mother–calf pair). The number of escorts ranged from 2 to as many as 11. In many cases it was not possible to measure all animals in a group, especially if the group was large, but we did make complete measurements of all members for 6 of the 12 groups. The principal escort was the largest animal measured in 8 of the 12 groups and the second largest (or tied for second) in 3 of the groups. In the one remaining group, the principal escort was sixth largest of 11 measured escorts. These within-group data provide strong support for the effectiveness of size in direct male–male competition among humpback whales.

Figure 1 also shows that there is a wide range of sizes of single escorts of a mother-calf pair and a wide range of sizes of male partners. Six (15%) of the single escorts were of probable immature size (less than 11.3 m) as were seven (41.2%) of the male partners.

We were only able to obtain measurements of eight singers. Inasmuch as the data for singers are based on a comparatively small sample, they should be treated as preliminary. One singer measured 11.29 m and may have been sexually immature, but the rest were 11.96 m or longer. These data suggest that singers may be, on average, sexually mature, but further observations and measurements are necessary, as visual observations suggest a broader size range, including smaller sizes, than that shown here.

Discussion

The principal escort has been defined as the male occupying and defending the position closest to the lone female within a competitive group of males (Tyack and Whitehead 1983). Our measurements of body size within these groups revealed that principal escorts were, on average, not only significantly larger than secondary escorts, but within the limits of the number of groups we examined, they tended to be the largest or second-largest male in the group. Further, the distribution of sizes of principal escorts, compared with distributions for secondary escorts, single escorts, and male partners, was heavily skewed toward larger sizes. Based on their size, all 17 principal escorts that we measured had a 0.81 probability or better of being sexually mature (Fig. 2), according to extrapolations of size measurements of North Pacific humpback whales reported by whaling biologists (Omura 1955; Nishiwaki 1959, 1962). Thus, like males of many other species (e.g., Davies and Halliday 1978; Clutton-Brock et al. 1982; Modig 1996), male humpback whales likely gain an advantage in physical competition from large body size.

In contrast to principal escorts, almost one-third of the 68 secondary escorts we measured, based on their size, had a 0.5 or lower probability of being sexually mature. One was only 9.1 m in length and was likely a yearling. Several others appeared to be, at best, of juvenile size. What were these smaller, apparently sexually immature males doing within these competitive groups? Our observations of these groups, extending over many years, affirm that not all of the whales present exhibit agonistic or challenging behaviors. Clearly, some tend to remain on the periphery of the group, at times

Table 3. Comparisons of sizes of measured male humpback whales according to their social role within competitive groups containing a single female without a calf.

Date	Pod composition	Social role	No. measurements	Mean length (m)	Rank
1998-03-05	NA10E	P	1	12.96	1
		S	1	12.27	2
		S	1	11.96	3
		S	1	11.70	4
1998-03-08	NA6E	S	1	12.45	1
		P	1	12.01	2
		S	1	11.78	3
		S	1	11.40	4
		S	1	10.23	5
		S	2	9.03	6
1999-02-06	NA2E	P	1	12.31	1
		S	3	12.22	2
1999-02-24	NA11E	S	2	13.15	1
		S	1	12.79	2
		S	3	12.72	3
		S	5	12.67	4
		S	2	12.30	5
		P	4	12.20	6
		S	1	11.96	7
		S	3	11.95	8
		S	7	11.86	9
		S	2	11.43	10
		S	2	10.13	11
1999-03-22	NA2E	P	3	11.92	1
		S	1	9.96	2
1999-03-23	NA5E	P	3	11.76	1
		S	4	11.42	2
1999-03-25	NA6E	P	5	13.34	1
		S	1	13.01	2
		S	3	12.83	3
		S	1	11.71	4
		S	2	11.68	5
		S	1	10.97	6
1999-03-25	NA5E	S	3	12.07	1
		P	2	11.88	2
		S	2	11.40	3
1999-03-26	NA7E	S	1	12.60	1
		P	2	12.53	2.5
		S	2	12.53	2.5
		S	1	12.26	4
		S	1	11.91	5

Note: NA, nuclear animal (female); E, escort; P, principal escort; S, secondary escort.

Table 4. Comparisons of sizes of measured male humpback whales according to their social role within competitive groups containing a single female with a calf.

Date	Pod composition	Social role	No. measurements	Mean length (m)	Rank
1999-02-17	Mc3E	P	1	14.03	1
		S	1	10.96	2
1999-03-10	Mc6E	P	1	12.79	1
		S	1	11.45	2
		S	1	11.23	3
		S	1	11.05	4
		S	1	10.06	5
1999-04-04	Mc3E	P	2	12.43	1
		S	1	12.10	2
		S	1	10.67	3

Note: M, mother; c, calf; E, escort; P, principal escort; S, secondary escort.

many whale lengths removed from the "action". Many of these apparently sexually immature secondary escorts may be attracted to a competitive group because of an evolved male predisposition, but their function in the group may be essentially as passive participants in a learning situation, observing the social interactions that may be instructive for their future participation and performance. Further research is necessary to determine whether the whales that are consistently on the perimeter of the competitive group are significantly smaller, on average, than those secondary escorts that exhibit agonistic behaviors directed toward each other or toward the principal escort.

Principal escorts were also significantly larger, on average, than either the single escort of a mother–calf pair or the male partners. The latter groups did not differ significantly in size from each other, nor from the mean size of secondary escorts. As with the secondary escorts, the percentages of single escorts and male partners having probabilities of sexual maturity of 0.5 or lower were large: approximately 20% of the single escorts of a mother–calf pair and 53% of the male partners. Spitz (1999) reported that many female partners were also small. Of 16 female partners measured, 12 were 11.9 m or less in length. Nishiwaki (1959, 1962) found that 50% of the females 11.9 m in length were sexually immature. Hence, it appears that large percentages of male and female partners in dyads are immature. Many dyads, therefore, may consist of juveniles and subadults. The presence of these smaller animals on the winter grounds may primarily reflect the continuation of the seasonal migratory behavior they experienced as calves (e.g., Dawbin 1966), but they may also gain opportunities to learn how to participate in the social network that leads to successful reproduction in later years.

A smaller male escort found in association with a mother–calf pair may benefit from the relatively benign social learning opportunity. The larger escorts consorting with a mother–calf pair may have encountered a mother that was ovulating post partum and therefore remained with her. Alternatively, the mother may be the predominant class of female available

(especially late in the season; Herman et al. 1980) and therefore worth accompanying. At the same time, we cannot rule out the possibility that these larger males are unsuccessful competitors.

The role of the singer remains enigmatic. All but one of the eight singers we measured were of sizes that represented a 0.9 probability or greater of sexual maturity (the outlier had a 0.5 probability). However, we cautioned earlier that our sample of singers was small, and further measurements may reveal that the distribution of sizes of singers is broader than is depicted here. Inasmuch as singing rarely directly attracts females to the singer (Mobley et al. 1988; Darling and Bérubé 2001; cf. Medrano et al. 1994), how does singing by sexually mature males contribute to the reproductive success of these animals? What function might be served by smaller males, if they are in fact participants in singing? How does the size of singers compare with the size of those males that approach singers (Darling and Bérubé 2001)? Much work needs to be done to answer these questions but the characteristic communal singing of the males is reminiscent of a lektype system, as was first proposed by Herman and Tavolga (1980) and later modified by Clapham (1996). Communal displays advertise the presence of multiple males and can serve to attract females to an area.

Our preliminary measurements (see Spitz 1999) suggest that the female in the competitive group (the nuclear animal) is sexually mature and significantly larger, on average, than females in dyads, but not significantly larger than mothers. However, the finding of whaling biologists that postpartum ovulation is relatively infrequent among lactating humpback whales compared with nonlactating females (Chittleborough 1955*b*, 1958) suggests that mothers may be a less desirable reproductive target for these large, sexually mature males than is the nuclear animal in the competitive group. Thus, males 11.9 m or longer (Fig. 1) constituted 76% of the sample of principal escorts but only 42% of the sample of single escorts of a mother–calf pair. However, as was noted, there clearly are seasonal changes in the relative numbers of adult females without a calf and females with a calf present on the winter grounds, and the implications of this for the within-season strategies adopted by the large males need study. Newly pregnant females are among the first to leave the winter grounds and females with a calf are among the last groups (Chittleborough 1965; Nishiwaki 1962, 1966; Dawbin 1966; Herman et al. 1980; Craig 2001). Hence, as the season progresses, large, sexually mature males should be found more frequently among the escorts accompanying mother–calf pairs. We may also see that the characteristics of the dyads change over the season, with larger males being more commonly found in that role later in the season. Whaling data have shown that immature males typically migrate back to the summer grounds earlier than do mature males (Dawbin 1966). At present, however, we do not have enough size data conditioned by time of the season to be able to make firm statements about these hypotheses.

As noted by Frankel et al. (1995), it is unlikely that male humpback whales develop long-term dominance hierarchies on the winter grounds because of their extensive movements within and between islands and the impermanence of social affiliations (Mobley and Herman 1985). However, the differences in size and positioning between principal and secondary escorts suggest that the principal escort occupies at least a temporary role as the dominant male. Nonetheless, some of the secondary escorts are also large, and some may eventually assume the role of principal escort by displacing the current occupant of that position or by establishing themselves in that position in another competitive group (Tyack and Whitehead 1983; personal observations). Because of apparent inappetence on the winter grounds (Chittleborough 1965; Dawbin 1966), the whales must rely on their accumulated fat reserves to meet metabolic requirements. Consequently, an active role as either a principal escort or a challenger in a competitive group can result in a costly expenditure of energy. Nevertheless, the competitive group appears to be a major reproductive unit, bringing together a receptive female and potential mates. For male humpback whales, then, the benefits of participating in a competitive group may in many cases outweigh the costs. For the female, the competitive group may function as a sorting process, allowing her to exercise choice among potential mates.

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