

Male mate choice and male–male competition coexist in the humpback whale (*Megaptera novaeangliae*)

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Abstract: Male humpback whales (*Megaptera novaeangliae*) outnumber females on the winter grounds and compete physically for proximity to females. Analyses of identification photographs collected in Hawai'i from 1976 through 1995 and scan samples collected in 1998 showed that (i) reproductive potential (calving rate) for the following winter was greater for females without a calf than females with a calf, (ii) females without a calf were less likely to be found alone and more likely to be found in large pods than females with a calf, (iii) *individual* females were found in larger pods when without a calf than when with a calf, (iv) the probability of females with a calf being escorted by one or more males increased as the reproductive season progressed, and (v) head lunges occurred more commonly in all-adult pods than in pods containing a calf. We concluded that male humpback whales associate preferentially with females with high reproductive potential, that the attractiveness of *individual* females varies with their status (with a calf versus without a calf), that males become progressively less choosy over the course of the reproductive season as females without a calf become increasingly rare on the winter grounds, and that males expend more energy in competition over females without a calf than females with a calf.

Résumé : Chez les baleines à bosse (*Megaptera novaeangliae*), le nombre de mâles excède le nombre de femelles dans les quartiers d'hiver et les mâles se font compétition physiquement pour s'approcher des femelles. L'analyse de photographies d'identification prises à Hawaï entre 1976 et 1995 et des échantillons de survol en 1998 démontrent que (i) le potentiel reproducteur (taux de mise bas) à l'hiver suivant est plus élevé chez les femelles sans petit que chez les femelles avec un petit, (ii) les femelles sans petit ont une probabilité moins grande de se retrouver seules et une probabilité plus élevée de faire partie de grandes bandes que les femelles avec un petit, (iii) les femelles fréquentent de plus grands bancs quand elles n'ont pas de petit, (iv) la probabilité qu'une femelle avec un petit soit escortée par un ou plusieurs mâles augmente à mesure qu'avance la saison de reproduction, (v) les coups de tête sont plus fréquents dans les groupes composés uniquement d'adultes que dans les bandes comptant un petit. Donc, les mâles de la baleine à bosse s'associent de préférence à des femelles qui ont un potentiel reproducteur élevé; l'attrait d'une femelle en particulier varie avec son statut (avec ou sans petit); les mâles deviennent progressivement moins difficiles dans leur choix à mesure qu'avance la saison de reproduction et que les femelles sans petit se font de plus en plus rares dans les quartiers d'hiver; enfin, les mâles dépensent plus d'énergie lorsqu'ils font compétition pour des femelles sans petit que pour des femelles avec un petit.

[Traduit par la Rédaction]

Introduction

The suggestion that one sex is competitive and the other choosy in mating behavior was first put forth in Darwin's

(1981) theory of sexual selection. Typically, males produce large numbers of microgametes and exhibit less total parental investment than females, suggesting that male reproductive success is limited only by the number of females that can be inseminated (Bateman 1948; Trivers 1972). Thus, males generally compete with each other for mating access to females. Conversely, females generally produce limited numbers of energy-rich macrogametes, and their total parental investment is usually greater than that of males. This leads to the conclusion that, in general, a female's reproductive success is limited not by the number of sexual partners she has, but by the number of surviving offspring that she successfully raises (Bateman 1948; Trivers 1972). The traditional view is that the sex making the higher parental investment (usually the female) will be discriminating in its choice of mates because it has more to lose from mating with a suboptimal partner. However, it has become apparent that there are exceptions to the general rule of male–male competition and female choosiness. In some species the typical

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sex roles are reversed, with males assuming parental duties and females copulating with many males (for a review see Andersson 1994, Chapter 7). However, it is becoming clear that even in cases where the traditional sex roles are not reversed, the notion of competitive males and choosy females is overly simplistic.

In a seminal paper, Dewsbury (1982) argued that although the single spermatozoon is the functional unit at the moment of fertilization, it is not the functional unit in the evolution of mating behavior. Spermatozoa are delivered not individually but in batches of several million, and the ejaculate also contains potentially costly accessory-gland secretions that are likely to be limited in supply. In a study that provides rare insight into the energetic costs of semen production, Olsson et al. (1997) reported that the rate of body mass loss in male adders (*Vipera berus*) was as high during the phase when the males were immobile and building up sperm supplies as it was when the males were mobile and engaging in reproductive behaviors such as mate searching, combat, and courtship. In most mammals, the production of sperm and seminal fluid is believed to be more expensive energetically than the production of an ovum (Snowdon 1997). High sperm counts appear to be required for successful insemination (e.g., 120–125 million in domestic sheep; Synott et al. 1981). However, sperm supplies become depleted after repeated ejaculations, as has been demonstrated in both birds and mammals (Squires et al. 1979; Synott et al. 1981; Birkhead 1991). Thus, there are limits to semen production and it is clear that more costs are incurred during male gamete delivery than has often been assumed. Consequently, as Dewsbury (1982) pointed out, some degree of male discrimination between mates may be expected even in species in which males are promiscuous.

There are additional reasons to expect some degree of choosiness on the part of males. Male mate choice may be predicted wherever there is variance in female reproductive potential (Andersson 1994; Owens and Thompson 1994). Assuming that a male cannot mate with all reproductive females in a given population, a male choosing randomly between females with differing probabilities of conceiving will, on average, have fewer offspring than a male favoring more fertile females (Altmann 1997). Although choosiness is often considered to be the opposite sex role to competition (e.g., Emlen and Oring 1977), variance in mate quality can favor the evolution of selectivity in mate choice by members of the competitive sex (Andersson and Iwasa 1996). Thus, competition and mate choice can coexist in one sex, as is demonstrated by the growing evidence of this phenomenon in crustaceans (Jormalainen et al. 1994), fishes (Sargent et al. 1986), insects (Van Dongen et al. 1998), amphibians (Arntzen 1999), birds (Owens et al. 1994), and mammals (Smuts 1987).

In this study, we explore the possibility that male mate choice coexists with male–male competition in the humpback whale (*Megaptera novaeangliae*). Humpback whales migrate seasonally between high-latitude summer feeding areas and low-latitude winter breeding areas (Chittleborough 1965; Dawbin 1966). Reproduction is strongly seasonal, with peaks of spermatogenesis and ovulation evident during the winter (Chittleborough 1954, 1955; Symons and Weston 1958; Nishiwaki 1959). In humpback whales, as in most cetaceans, mating behavior is poorly understood. During the winter repro-

ductive season females both with and without a calf are serially and simultaneously escorted by multiple males (Tyack and Whitehead 1983; Baker and Herman 1984) and social groupings are transient (Mobley and Herman 1985). Because humpback whale copulation has never been observed directly, it is not clear whether male escorts are prospecting for receptive females or practicing postcopulatory mate guarding (Mobley and Herman 1985; Brown and Corkeron 1995; Clapham 1996), or both. However, it is clear that parental investment by females is much greater than that by males, who contribute sperm only, and that the operational sex ratio on the winter grounds is greatly skewed towards males (Herman and Tavalga 1980; Brown et al. 1995; Craig and Herman 1997; Palsboll et al. 1997; Smith et al. 1999). Thus, as would be predicted on theoretical grounds, the males that escort females generally exhibit aggressive behaviors towards each other as they seek close spatial proximity to a female (Darling et al. 1983; Tyack and Whitehead 1983; Baker and Herman 1984). The most commonly observed aggressive behavior is the head lunge, during which a whale thrusts its head forwards out of the water, often with the throat area inflated (Baker and Herman 1984). In some cases, forceful contact occurs between competing males, resulting in bloody wounds (Herman and Tavalga 1980; Darling et al. 1983; Tyack and Whitehead 1983; Baker and Herman 1984). The apparent importance of physical competition relative to sperm competition in the mating system of humpback whales is also predicted from the small size of the testes in relation to body size (Brownell and Ralls 1986).

The gestation period of humpback whales is between 11 and 12 months, and lactation may continue for as long as 10.5 months (Matthews 1937; Chittleborough 1958). Examination of commercial whaling catches revealed that some females suckling a recently born calf were simultaneously pregnant with their next calf, indicating that postpartum estrus and conception had occurred (Matthews 1937; Chittleborough 1958). Chittleborough (1958) reported that 8 of 19 (42.1%) lactating females were pregnant compared with 67 of 75 (89.3%) nonlactating females. Although annual births do occur in this species, the modal interbirth interval is 2 years (Chittleborough 1958; Baker et al. 1987; Clapham and Mayo 1990; Glockner-Ferrari and Ferrari 1990; Barlow and Clapham 1997). One probable reason for infrequent annual births is that mysticete lactation is energetically very expensive (Lockyer 1981), and female humpbacks ending lactation are likely to be in poor physical condition relative to nonlactating females. These lines of evidence converge to suggest that the reproductive potential of females varies with their status during the reproductive season; specifically, reproductive potential for the following year is lower in lactating females than in adult females without a calf.

Humpback whale winter grounds are generally located in waters of low productivity (e.g., Herman 1979), and whaling data revealed that humpback whales generally do not feed during their residency on the winter grounds (Nishiwaki 1959; Chittleborough 1965; Dawbin 1966). The energetic constraints faced by males occupying a winter habitat devoid of an exploitable food resource suggest that males are more likely to expend energy in competition over females with high reproductive potential than over females that are less likely to bear a calf the following year. Clapham (1996)

noted that although females with a calf are often at the center of pods of competing males in Hawaiian waters, they are less frequently found in competitive pods in the West Indies. He suggested that the rarity of calves in competitive pods in the West Indies may reflect a preference by males for females that are not lactating. However, no data were available to allow a systematic investigation of this possibility. In a Master's thesis, Gabriele (1992) reported that the distribution of pod sizes in which females with a calf were found off Hawai'i was significantly different from the distribution of pod sizes in which females with no calf were found. More detailed statistical analyses of these data were not conducted, but Gabriele (1992) did suggest that the difference was probably best accounted for by the observations that fewer females with no calf were found alone than were females with a calf, and more females with no calf were found in large pods than were females with a calf. The possibility that male aggression levels differ between pods that contain a calf and those that do not contain a calf has never been evaluated. However, if males preferentially expend energy in competition over females without a calf it follows that, all other things being equal, aggressive and energetically more expensive behaviors such as head lunging should be exhibited less frequently in pods that contain a calf than in pods that do not contain a calf.

Johnstone (1997) developed a model of mutual mate choice which predicts that because high-quality individuals find a partner and drop out of the mating pool more quickly than lower quality individuals, the mean quality of unmated individuals will decline as the reproductive season progresses. Individuals that may have been choosy near the start of the season will become progressively less choosy over the course of the season. This is relevant to humpback whales because females without a calf tend to leave the winter grounds earlier than males and females with a calf (Chittleborough 1965; Dawbin 1966, 1997). Consequently, females without a calf become increasingly rare on the winter grounds as the reproductive season progresses. Males, however, will continue to seek mating opportunities throughout their residency on the winter grounds. This raises the possibility that males become progressively less choosy over the course of the winter reproductive season. This would be consistent with Mobley and Herman's (1985) finding that the size of pods containing a calf increases linearly as the reproductive season progresses.

In this study we use data collected from boat- and shore-based platforms in Hawai'i, the principal winter ground for the majority of North Pacific humpback whales, to test the hypothesis that male humpback whales do not associate with females at random, but associate preferentially with females that have high reproductive potential for the following year. We begin by confirming for our dataset that reproductive potential for the following year is greater for females with no calf than for females with a calf in any given year. We then examine not only the mean pod sizes in which these two classes of female were found, but also their relative probability of being found alone or in large pods (those containing four or more adults). We conduct a within-subjects analysis to determine whether the apparent attractiveness of individual females varies with their reproductive status. We examine whether females with a calf are escorted with increasing frequency as the season progresses. Finally, we investigate

whether head lunging is more likely to occur in pods without a calf than in pods that contain a calf.

Methods

Data were collected by staff of the Kewalo Basin Marine Mammal Laboratory from both boat- and shore-based platforms in the Hawaiian Islands.

Boat data

Individual humpback whales can be identified by the unique ventral pigmentation of their tail flukes, together with the serrations on the trailing edge (Katona et al. 1979). Photographs of humpback whale tail flukes were collected in the Hawaiian Islands between January and April of each year from 1976 through 1995. Data collection focused on Maui and the island of Hawai'i ("the Big Island"), but some photographs (ca. 1%) were also obtained off Niihau, Oahu, and Penguin Bank. The whales were followed in small boats and photographed with a 35-mm camera equipped with a telephoto lens, typically with a focal length of 300 mm. Whales were generally followed for as long as was necessary to obtain a good fluke photograph for each whale in the pod. There was no deliberate selection of particular pod types for photography. The best photograph of each whale in a given pod was assigned a unique observation number and classified by pigmentation. Each photograph was then compared visually with all others in the same color category and any matching photographs were allocated a common "resight" number that served to identify a particular whale.

Because the sex of humpback whales generally cannot be determined from surface observations, sex was inferred from the social role. Any whale observed in consistently close proximity to a calf was considered to be its mother, and therefore female. Any whale of adult size (judged by eye) escorting a female with a calf was assumed to be male, and any whale observed to be singing was considered male. Underwater observations of the genital region and molecular determination of sex from skin biopsies have validated these assumptions (Glockner 1983; Glockner-Ferrari and Ferrari 1985; Clapham et al. 1992; Medrano et al. 1994). When sex was determined for a given individual, all previous identifications were updated.

All data (e.g., date, social role, pod composition) associated with each photograph were stored and analyzed in SAS (SAS Institute Inc. 1999). Data were considered separately for the Big Island and Maui because pod characteristics differ between these two areas (Bauer 1986; Craig 2001). Calculations of pod size (expressed as the number of adults) deliberately excluded all calves and juveniles. The few sightings of females known to be in late pregnancy were omitted from analysis, and for all other females it was assumed that if they were photographed without a calf in a given year they did not give birth that year. This assumption is supported by a collaborative study based on data collected in Hawai'i and Alaska by eight different research groups. A total of 2179 sightings of 314 individually identified females yielded only 4 cases in which a female was identified initially without a calf in Hawai'i and subsequently with a calf in either Hawai'i or Alaska during the same reproductive year (Gabriele et al. 2001).

Table 1. Mean number of adults (including the female) in humpback whale (*Megaptera novaeangliae*) pods containing a known female of adult size.

	No. of adults in pods containing a female with a calf			No. of adults in pods containing a female with no calf		
	Mean	SD	<i>N</i>	Mean	SD	<i>N</i>
Overall	1.99	0.95	398	2.82	1.73	98
Maui	2.07	0.97	173	3.31	2.28	42
Big Island	1.93	0.94	222	2.45	1.03	55

Note: Data are presented separately for pods that contained a female with a calf and pods that contained a female with no calf. Overall data include a small number of pods that were photographed in areas other than Maui and the Big Island.

Shore data

Between 14 January and 17 April 1998, land-based observations were conducted from an elevated (56.46 m) observation site ("Puu Pilau") located at 156°38'03"W, 20°49'49"N on the west coast of Maui. The study area encompassed all waters within a 6.5-km radius of Puu Pilau. Data were collected using a scan-sampling procedure (Altmann 1974; Martin and Bateson 1993). Scan samples lasted for 15 min to increase the probability that any pod in the sampling area would be at the surface at some time during the scan sample, but each pod was counted once only. Scan samples were collected at standard times daily or near-daily between 09:15 and 17:15, weather permitting. Scan samples included in this study were separated by at least 3 h, allowing sufficient time for whales counted in the previous scan to have moved out of range of the shore station, assuming normal swimming speeds (e.g., Helweg and Herman 1994; Smultea 1994). This enabled each scan sample to be treated as independent.

A Sokkia DT-6 theodolite was used to obtain position "fixes" on all pods sighted by the observer during a scan; the angles of declination and azimuth were used to calculate the range and bearing of each pod from the shore station (e.g., see Wursig et al. 1991). Obtaining a precise position fix also minimized the possibility that any pod was counted more than once during the same scan. Group composition was determined using the 30-power magnification of the theodolite spotting scope, which enabled the operator to identify reliably the presence or absence of calves in all pods within the 6.5-km sampling area. All pods more than 6.5 km from the shore station were discarded from the dataset. The theodolite operator also used the spotting scope to note all observations of head-lunging behavior. Head lunging was defined as occurring when a whale thrust its head forwards out of the water, typically with the throat area inflated (see Baker and Herman 1984; Pack et al. 1998). It was assumed that head lunging, which occurs at the surface, reflects overall aggression and energy expenditure by males above and below the surface.

Data were analyzed in SAS. Prior to this analysis, all data were screened for potential observer effects and biases resulting from sea state or other environmental conditions (Craig 2001). To investigate seasonal trends, data were grouped by fortnight of the year. Fortnight 1 extended from 1 to 14 January, fortnight 2 from 15 to 28 January, and so forth.

Results

Boat data

Reproductive potential

There were few sightings of females in consecutive years, as has been reported previously for a subset of these data (Craig and Herman 1997). When only the 22 cases in which sightings occurred in 2 consecutive years were considered, the probability that a female with no calf would be seen the following year with rather than without a calf was 0.75 (9 of 12 cases). In contrast, the probability that a female with a calf would be seen the following year with another calf was only 0.10 (1 of 10 cases) (Fisher's exact test, $N = 22$, $p = 0.0037$). Thus, these data support the suggestion that reproductive potential for the following year is higher for females with no calf than for females with a calf.

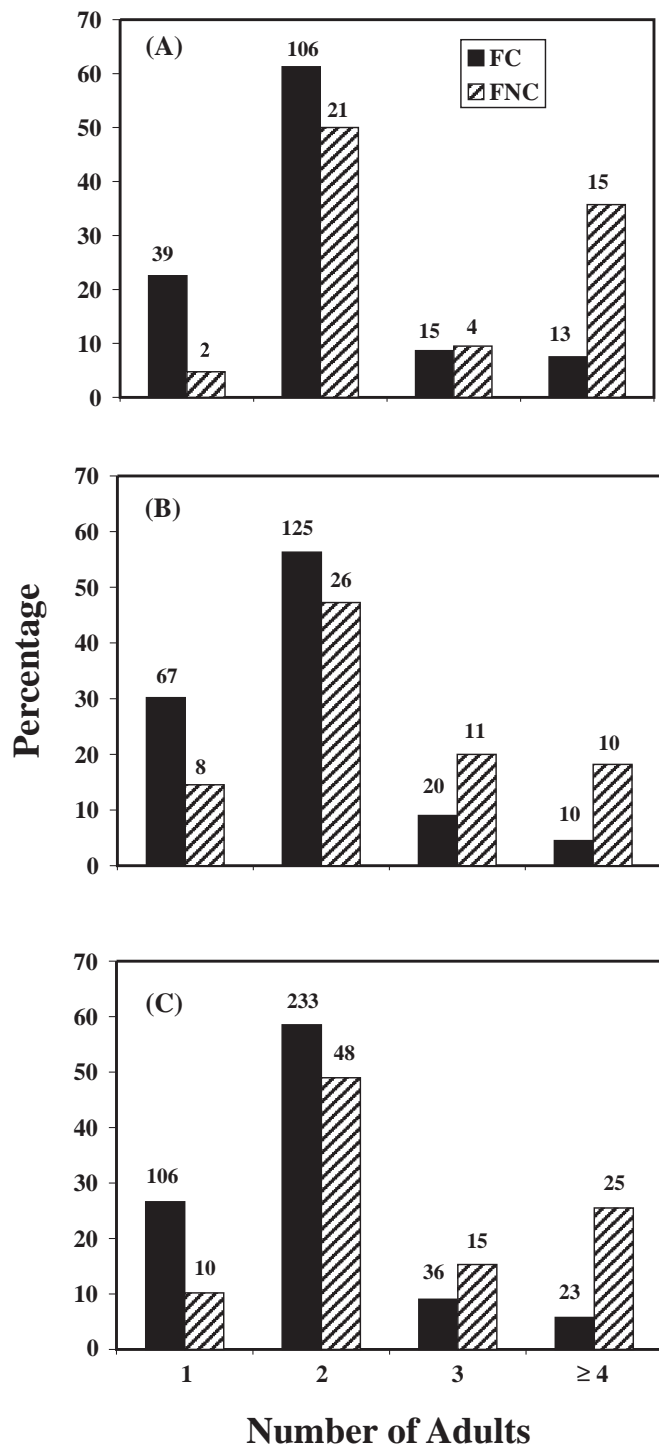
Pod composition

No pod contained more than one known female. Table 1 summarizes the mean numbers of adults (including the female) in pods containing a female with a calf and in pods containing a female with no calf. Overall, pods containing a female with no calf (mean = 2.82, SD = 1.73, $N = 98$) were larger than pods containing a female with a calf (mean = 1.99, SD = 0.95, $N = 398$). As Table 1 shows, the same trend was evident when data were separated by island location. Wilcoxon's rank sum tests revealed that these differences in pod size were significant overall ($S = 31\ 036.0$, $df = 1$, $p = 0.0001$), for Maui ($S = 5987.5$, $df = 1$, $p = 0.0001$), and for the Big Island ($S = 9544.00$, $df = 1$, $p = 0.0001$).

Figure 1 summarizes the distribution of sizes of pods in which females were found. It is clear that females with no calf were unlikely to be alone: overall, females with no calf were unaccompanied by another adult on only 10.20% of occasions compared with 26.63% for females with a calf (Fisher's exact test, $N = 496$, $p = 0.00046$). Similar differences were found when data were considered separately for Maui (Fisher's exact test, $N = 215$, $p = 0.00764$) and the Big Island (Fisher's exact test, $N = 277$, $p = 0.018$). Although only 4.76% of females with no calf were alone off Maui compared with 14.55% off the Big Island, this regional difference was not significant (Fisher's exact test, $N = 97$, $p = 0.179$). Similarly, females with a calf were less likely to be unescorted off Maui (22.54%) than off the Big Island (30.18%), but this difference was not significant (Fisher's exact test, $N = 395$, $p = 0.109$).

Females with no calf were more likely to be in large pods than were females with a calf: overall, 25.51% of sightings of females with no calf featured pods containing four or more adults compared with only 5.78% of sightings of females with a calf (Fisher's exact test, $N = 496$, $p < 0.0001$). When the data were considered separately by region, similar results were obtained. Off Maui, in 35.71% of sightings of females with no calf, they were in pods of four or more adults compared with only 7.51% of sightings of females with a calf (Fisher's exact test, $N = 215$, $p < 0.0001$). Off the Big Island, in 18.18% of sightings of females with no calf, they were in pods of four or more adults compared with only 4.50% of sightings of females with a calf (Fisher's exact test, $N = 277$, $p = 0.00162$).

Fig. 1. Distribution of pod sizes (expressed as the number of adults) in which females with a calf (FC) and females with no calf (FNC) were found off Maui (A), the Big Island (B), and overall (C). Numbers above the columns are sample sizes.



Within-subjects comparison

The foregoing statistical tests treated each pod as an independent sample. Because the vast majority of individuals in this dataset were identified only once within and across seasons (see Craig and Herman 1997; Craig 2001), the presence

of some individuals in more than one pod should have had minimal impact on the results. However, to permit a within-subjects comparison of pod size for individual females as a function of reproductive status, we selected all females ($N = 50$) that had been identified as being with and without a calf in different years. For each of these 50 females we compared the mean pod size (expressed as the number of adults) for all sightings as a female with a calf and all sightings as a female with no calf. If individual females were equally attractive or receptive to males whether they were accompanied by a calf or not, we would expect no systematic differences in pod size as a function of reproductive status. However, mean pod sizes were larger when without a calf than with a calf for 31 females, mean pod sizes were equal in both conditions for 13 females, and mean pod sizes were smaller when without a calf than with a calf for only 6 females (sign test, $p < 0.001$). Thus, individual females tended to be found in larger pods when they were without a calf than when they were with a calf.

Shore data

Seasonal trend in probability of being escorted

A total of 181 pods containing a calf were counted in the 100 scan samples that comprised the dataset. Figure 2 illustrates the seasonal trend in proportion of females with a calf that were escorted by one or more males. A regression of the proportion of females with a calf that were escorted on fortnight revealed a significant positive gradient ($y = 0.079x + 0.345$, $t_{[6]} = 5.06$, $p = 0.0039$). Only one pod containing a calf was observed in the last fortnight of data collection, however. When this fortnight was omitted, regression analysis still showed a significant positive gradient ($y = 0.075x + 0.360$, $t_{[5]} = 3.43$, $p = 0.0264$).

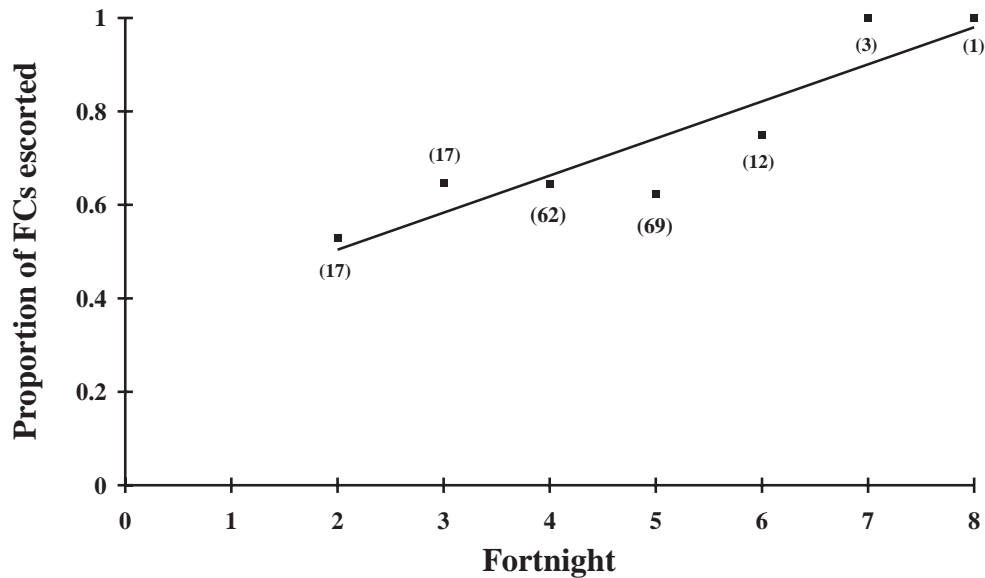
Head lunges

Head lunges were recorded for only 27 pods, of which 23 (85.19%) did not contain a calf and only 4 (14.81%) contained a calf (Fisher's exact test, $N = 779$, $p = 0.014$). However, sample sizes were too small to permit a systematic comparison of the incidence of head lunging in pods that contained a calf and pods of equivalent size that did not contain a calf.

Discussion

The results confirmed that reproductive potential for the following year is higher for females with no calf than for females with a calf. No pod contained more than one known female, and females with no calf were found in significantly larger pods than females with a calf. Females with no calf were significantly less likely to be found alone and more likely to be found in large pods (i.e., those containing four or more adults) than were females with a calf. Moreover, a within-subjects comparison revealed a significant tendency for individual females to be found in larger pods in the years when they had no calf than in the years during which they had a calf. There was a significant seasonal increase in the probability of a female with a calf being escorted, and head lunges were significantly less likely to be observed in pods that contained a calf than in all-adult pods, although the

Fig. 2. Proportion of females with a calf (FC) that were escorted by one or more males for each fortnight of shore data collection. Numbers in parentheses are sample sizes.



small sample size precluded a comparison of pods equated for size.

These results collectively suggest that (i) males preferentially escort those females with the highest reproductive potential, (ii) individual females attract more males when without a calf than with a calf, (iii) males become progressively less choosy as the winter reproductive season progresses, and (iv) males expend more energy in competition over females without a calf than females with a calf. Thus, male humpback whales not only engage in physical competition for proximity to females (Tyack and Whitehead 1983; Baker and Herman 1984), but also exhibit mate choice. This finding adds to the gradually accumulating evidence from other taxa that choosiness and competition are not mutually exclusive sex roles, and that mating systems are more complex than has been traditionally assumed (Sargent et al. 1986; Smuts 1987; Jormalainen et al. 1994; Owens et al. 1994; Van Dongen et al. 1998; Arntzen 1999). The present study also provides further evidence that the behavior of cetaceans is not fundamentally different from that of their terrestrial counterparts, and can be predicted reasonably well using the principles that are applied to terrestrial species (see Clapham 1996).

The interpretation of courtship and mating behaviors presents special difficulties when the data do not permit a definitive conclusion to be drawn about the relative contributions of the two sexes to the results under discussion (e.g., see Eberhard 1990). In discussing the data presented here, we do not mean to imply that female humpback whales are simply passive recipients of male attention, with no control over their attractiveness to males. There may be behavioral or physiological cues from a female that influence whether or not she is actively pursued by males. The data presented here, therefore, may reflect the behavior of both males and females. Nonetheless, it appears that more males are attracted by females without a calf than are attracted by females with a calf. Thus, males do not escort females indiscriminately or at random.

It could be argued that females with a calf have lower

conception probabilities *because* they are less likely than females without a calf to attract males. Thus, there is some circularity in arguing that males are less likely to select them as mates because they have lower reproductive potential. However, there are good reasons to predict that even if males did not discriminate between females with calves and those without, the latter would still have greater reproductive potential. Chittleborough (1958) noted that female humpbacks demonstrating postpartum ovulation with conception would give birth the next year approximately 1 month later than females that were not in early lactation when they conceived. In other seasonally breeding mammals it has been shown that individuals born early in the reproductive season have survival advantages over those born later in the reproductive season (Clutton-Brock et al. 1988; Festa-Bianchet 1988; Le Boeuf and Reiter 1988; Berger 1989). Chittleborough (1958) went on to suggest that an annual calving cycle could not be maintained continuously by an individual humpback whale because she would end up giving birth progressively later each year.

It is also unlikely that an annual calving cycle could be maintained over many successive years because of the extreme energetic demands placed on the female. Lactation is particularly expensive energetically for mysticetes (Lockyer 1981), and the lack of an exploitable food resource on the winter grounds means that female humpbacks must metabolize stored energy reserves to sustain themselves and produce milk for their calves. Furthermore, because the timing of migration both to and from the feeding grounds varies according to reproductive status, females may spend approximately 2 months less in the feeding grounds when accompanied by their calf than they do when they have no calf (Dawbin 1966, 1997). Dawbin (1966) noted that females approaching the end of lactation yielded approximately half as much oil as was obtained from similarly sized females in late pregnancy caught at the same location. This provided clear physical evidence that the body condition of females during late lactation is relatively poor. For all these reasons,

if a female terminating lactation gives birth to a calf shortly thereafter and resumes lactation again, she may experience severe metabolic stress. Consequently, it is unlikely that a female could sustain this pattern of reproduction over many consecutive years. The maximum number of consecutive years over which females are known to have produced calves that survived through migration to the feeding grounds is 3 (Weinrich et al. 1993; Straley et al. 1994). An effective strategy for maximizing reproductive success over a female's lifetime may be to reduce the number of annual pregnancies and instead produce fewer offspring, each of which will have a higher probability of long-term survival than would offspring produced as a result of frequent annual pregnancies (Craig and Herman 1997). Thus, the evidence suggests that females with a calf would have lower reproductive potential for the next year than would females without a calf, even if males sought to mate with females at random.

If a female humpback does give birth in 2 successive years, the second calf may have lower reproductive success than a calf born after a longer interbirth interval. Wiley and Clapham (1993) reported that female humpbacks with interbirth intervals of 3 years or more, judged to be in superior body condition, appeared to bias their production of offspring towards males. However, the sex ratio of offspring produced by females with shorter interbirth intervals, judged to be in poor or average body condition, did not differ from parity. In species where male parental investment is negligible and variance in male reproductive success is high, a son in good condition when parental investment ends should have greater reproductive success than a sister in similar condition (Trivers and Willard 1973). Although this remains somewhat speculative for humpback whales, it does lend further support to the suggestion that a male who selectively allocates his sperm to females without a calf rather than females with a calf will have a greater representation of his genes in subsequent generations than a male who mates indiscriminately.

The seasonal increase in the probability that females with a calf will be escorted is most likely related to differences in migratory timing among different classes of whale. As mentioned earlier, female humpback whales without a calf tend to leave the winter grounds earlier than males and females with a calf (Chittleborough 1965; Dawbin 1966, 1997). Craig (2001) reported that for both Maui and the Big Island, the last date on which females without a calf were identified in any given year was significantly earlier than the last date on which males and females with a calf were identified. These data suggest that females without a calf become increasingly rare relative to females with a calf as the reproductive season progresses in Hawai'i. As the proportion of females without a calf declines, the cost to benefit ratio associated with searching for these females with high reproductive potential should change. Specifically, the expected future fitness gains from a continued search should decline (as proposed in Johnstone's 1997 model) until such time as the most cost-effective strategy for males is to escort females with a calf.

Possibly the behavior of female humpbacks contributes to this seasonal trend. It may be that females with a neonate are not receptive to males and avoid associating with them, but subsequently become less evasive and more receptive as their calf matures. There is little evidence bearing directly on this question. Neither the minimum nor the modal interval

between parturition and postpartum estrus is known. Smultea (1994) reported that off the Big Island, pods containing a calf tended to be found closer to shore and in shallower water than all-adult pods. She found that this trend was most pronounced in the latter part of the reproductive season (from mid-March onwards), and attributed it to increased avoidance of sexually active males by females with a calf at this time. This seasonal trend fits well with the present suggestion that males increasingly turn their attentions to females with a calf as the season progresses. Thus, the seasonal increase in the prevalence of escorted females with a calf is likely to be due, at least in part, to seasonal changes in male mating strategies.

There are similarities between the behavior of humpback whales on the winter grounds and the behavior of ungulates, which have a common ancestry with humpbacks (Berta and Sumich 1999). For example, Baker and Herman (1984) pointed out that the escorting behavior of male humpbacks is reminiscent of the tending behavior characteristic of many ungulate species. Like humpback whales, female bison (*Bison bison*), Rocky Mountain mule deer (*Odocoileus hemionus hemionus*), and white rhinoceros (*Ceratotherium simum*) are less likely to conceive in the years during which they are accompanied by a calf, and may therefore be characterized as being of lower reproductive value to males than are females without a calf. For each of these species, there is evidence that males preferentially associate with females with higher reproductive potential (Berger 1989; Margulis 1993; Rachlow et al. 1998; but see Wolff 1998). Moreover, it has been shown that female bison produce lower quality offspring when they reproduce in successive rather than alternate years (Green and Rothstein 1991), echoing the suggestion that female humpback whales may maximize their lifetime reproductive success by having relatively few annual pregnancies and instead concentrating their efforts on producing fewer, better quality offspring.

Reasons for males' mate preferences

Not only is the operational sex ratio in humpback whales skewed towards males (Herman and Tavalga 1980), the overall sex ratio of humpback whales on the winter grounds is also skewed towards males, with perhaps as many as 2.4 males to each female (Brown et al. 1995; Craig and Herman 1997; Palsboll et al. 1997; Smith et al. 1999). Given this information, mate choice by male humpback whales might be unexpected. However, it is important to consider the reproductive costs incurred by male humpback whales on the winter grounds. The lack of feeding on the winter grounds (Chittleborough 1965; Dawbin 1966; Nishiwaki 1966) suggests that male humpback whales lose considerable body mass during the reproductive season, in common with males of other seasonally reproductive mammals such as gray seals (*Halichoerus grypus*), red deer (*Cervus elaphus*), and northern elephant seals (*Mirounga angustirostris*) (Clutton-Brock et al. 1982; Anderson and Fedak 1985; Deutsch et al. 1990). Nishiwaki (1959) reported that the blubber thickness of both male and female humpback whales decreased over the course of the reproductive season. Even though males are not burdened with the energetic demands of lactation, it is clear that they are confronted with non-trivial energetic costs while on the winter grounds (Clapham 1996). It is likely, therefore, that

there is an element of endurance rivalry in the male–male competition of humpback whales. A male that selectively allocates his energetic expenditure to competition over females with high conception probabilities will be better able to endure a long period of residency on the winter grounds than will a male that rapidly expends energy in indiscriminate competition. Moreover, all other things being equal, a male inseminating a female with high reproductive potential should have greater reproductive success than a male inseminating a female with lower reproductive potential. Consequently, selective males are likely to have greater reproductive success than are males that indiscriminately expend valuable energy reserves in competition over females with lower reproductive potential.

As discussed earlier, Dewsbury (1982) proposed that the appropriate unit to be considered in the evolution of mating behavior is not the single gamete but rather the ejaculate, which contains millions of spermatozoa and also secretions from the accessory glands. The phenomenon of male sperm depletion has been documented in many ungulates, including goats (Fielden and Berker 1964), sheep (Synott et al. 1981), cattle (Almquist et al. 1958), and horses (Squires et al. 1979). For example, Synott et al. (1981) reported that the mean number of spermatozoa per ram ejaculate fell from 3900 million to 77 million over a period of 6 days. Given that the minimal level considered necessary for normal conception rates with artificial insemination is 120 million, it is clear that repeated ejaculations may depress sperm counts to a level unlikely to result in fertilization (Synott et al. 1981). The volume of humpback whale ejaculate delivered to females during copulation is not known, nor is it known how quickly males can replenish spermatozoa or other constituents of semen. However, based on measurements of sperm density in the vas deferens fluid of male humpback whales killed during the reproductive season, Chittleborough (1955) suggested that many sexually mature males could be tentatively classified as having low fertility. It is possible that many of these males had copulated shortly before being killed, thus depleting their reserves of spermatozoa. At the very least, the relatively low sperm counts of many of the humpbacks sampled by Chittleborough indicate that spermatozoa are not available in limitless quantities. It is also worth noting that spermatogenesis is seasonally regulated, and in the austral winter shows a clear peak during late July and August (Chittleborough 1955). Thus, humpback whales do not produce spermatozoa at maximal capacity for the entire winter reproductive season. Consequently, we might expect selection to favor males that allocate their limited supplies differentially among females with differing conception probabilities because such a tactic should result in greater reproductive success than would be obtained by copulating indiscriminately.

Directions for future research

It has been argued here that male humpback whales preferentially expend energy in competition over females with high reproductive potential, i.e., those without a calf. It follows that, all other things being equal, males in competitive pods without a calf should exhibit more energetic and aggressive behaviors than are exhibited by males in competitive pods containing a calf. The finding that head lunges

were more common in all-adult pods than in pods containing a calf was consistent with expectations. However, because it was not possible to control for the potential effects of pod size, this finding does not provide conclusive support. A more definitive answer to this question would be obtained by an empirical investigation of the aggressive behaviors observed in pods containing a calf and all-adult pods of equivalent size. However, even if aggression tends to be more frequent or intense in all-adult pods than in pods containing a calf, important exceptions are likely to occur when females with a calf actually enter postpartum estrus.

The present study has focused on the overall preference of males for females without a calf over females with a calf. However, males may prefer certain types of female within and across each reproductive class. For example, because larger individuals can accumulate more stored energy reserves than can be acquired by smaller individuals (Calder 1984), larger females should be better able than smaller females to provide their calves with energy-rich milk. Large female humpback whales are also likely to have a calf that is relatively large (Spitz 1999). Large calves may be more robust and likely to survive than smaller calves, as has been demonstrated for other species (Clutton-Brock et al. 1988). Thus, as proposed by Ralls (1976), larger mothers are most likely better mothers. If this is the case, male humpback whales may prefer large females to smaller females. Some preliminary evidence for this proposition comes from Spitz (1999). He measured females accompanied by competing males and found a significant correlation between the size of females without a calf and the number of males accompanying them. Further research into the role of size in mating preferences should increase our understanding of the dynamics of humpback whale mating behavior.

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