

# MIGRATORY TIMING OF HUMPBACK WHALES (MEGAPTERA NOVAEANGLIAE) IN THE CENTRAL NORTH PACIFIC VARIES WITH AGE, SEX AND REPRODUCTIVE STATUS

by

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## Summary

Humpback whales migrate seasonally between high-latitude summer feeding grounds and low-latitude winter breeding grounds. Identification photographs of humpback whales were collected in the Hawaiian Islands between 1977 and 1995, and sighting histories were compiled for individuals. Analyses revealed that (a) mean dates of first identification were significantly earlier for juveniles and females with no calf than for males and females with a calf off the Big Island, and significantly earlier for juveniles than for females with no calf, males and females with a calf off Maui; and (b) mean dates of last identification were significantly earlier for juveniles and females with no calf than for males and females with a calf off the

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Big Island, and significantly earlier for females with no calf than for males and females with a calf off Maui. A within-subjects comparison showed that the date of first identification tended to be later for individual females in the years when they had a calf than in the years during which they had no calf. It was concluded that (a) migratory timing varies as a function of age, sex and reproductive status, (b) migratory timing is intimately connected with reproductive success and (c) migratory timing has important consequences for our understanding of humpback whale behaviour on the winter grounds.

## Introduction

Migration is a behaviour common to many taxa, including insects, birds, fish, reptiles and mammals (Baker, 1978). By migrating, individuals are able to exploit the resources of habitats that would not be suitable on a permanent basis (Aidley, 1981). Historically, migratory behaviour was seen as an all-or-nothing product of the genotype: individuals were either genetic migrants or genetic non-migrants (Baker, 1982). However, it has become clear that migratory behaviour is more complex than was previously assumed. In many species there are differences in migratory behaviour as a function of age, sex and/or reproductive condition (*e.g.* Swartz, 1986; Kjellen, 1992; Otahal, 1995; Wiig *et al.*, 1996; Stewart, 1997; Woodrey & Chandler, 1997; Dittman & Becker, 2003; Yosef *et al.*, 2003). Here, we investigate whether these factors play a significant role in the migratory timing of humpback whales (*Megaptera novaeangliae*) in the central North Pacific.

Humpback whales, like most mysticetes, perform extensive, seasonal migrations between high-latitude summer feeding grounds and low-latitude winter breeding grounds (Matthews, 1937; Chittleborough, 1965; Dawbin, 1966; Baker *et al.*, 1986; Katona & Beard, 1990). Females are believed to conceive during the winter season on or en route to the winter grounds, and return to give birth to a single calf the following winter after a gestation period of 11-12 months (Matthews, 1937; Chittleborough, 1958). The mean length of lactation reported by Chittleborough (1958) was 10.5 months, and most mothers and calves have separated permanently by the time the calf is one year old (Clapham & Mayo, 1987, 1990). Migration to the winter grounds represents a considerable energetic investment. Although migratory swimming itself arguably incurs no more locomotory costs than does swimming within a more restricted locale (Corkeron & Connor, 1999), the lack of feeding on the winter grounds and the rarity of feeding during much of the migration mean that humpbacks must subsist on stored fat reserves for

extended periods of time (Nishiwaki, 1959; Chittleborough, 1965; Dawbin, 1966). Consequently, the differing energy requirements of different age and reproductive classes of whale are likely to exert considerable influence over migratory behaviour.

Biologists examining commercial whale catches found that humpback whale migrations to and from the winter grounds appeared to be loosely segregated on the basis of age, sex and reproductive condition (Nishiwaki, 1959, 1966; Chittleborough, 1953, 1965; Dawbin, 1966, 1997). Dawbin (1997) conducted the most extensive research into temporal segregation of humpback whales during migration, based upon studies of 65,600 humpbacks caught at various locations in the southern hemisphere. On average, the first whales to migrate to the winter grounds were females in late lactation, together with their yearling offspring. These females were then followed by immature whales of both sexes, mature males, resting females (*i.e.* mature females whose ovaries and mammary glands showed no evidence of recent activity) and, finally, females in late pregnancy. The earliest departure from the winter grounds was by mixed females (both resting females and those in early pregnancy) and immature whales of both sexes, followed by mature males and, finally, females in early lactation, accompanied by their recently-born calves. However, a recent study of humpback whales in the North Atlantic produced results that were inconsistent with those of Dawbin (1997). Stevick *et al.* (2003) reported that males were seen earlier than females on the West Indies winter grounds, and speculated that different selection pressures may have given rise to different schedules of migration in the northern and southern hemispheres. The present study of humpback migration in the North Pacific should help to clarify this issue.

The only published accounts suggesting temporally-segregated humpback whale migration in the North Pacific were provided by Nishiwaki (1959, 1966). Based on the composition of commercial whaling catches in Japanese waters, Nishiwaki (1959) stated that 'younger and smaller' whales tended to migrate to the Ryukyuan Islands wintering area at the beginning of the winter breeding season, and that 'immature' whales tended to migrate back to the feeding grounds earlier than did whales 'in lactating or mating stage' (p. 57). He also noted that by April, females with calves were predominant in Ryukyuan waters. Using photo-identification data collected during three breeding seasons in Hawaii, the principal winter grounds for North Pacific

humpback whales, Darling *et al.* (1983) failed to find any indication of differences in migratory timing among different classes of whale. However, Darling *et al.* also noted that their data were too sparse to permit a full investigation of this question. In an unpublished Master's thesis, Gabriele (1992) examined the timing of first and last identifications of humpback whales in the Hawaiian Islands between 1976 and 1989. She concluded that first and last identifications of females without calves occurred earlier in the season than did those of males and females with a calf.

In the present study, we extend the data set used by Gabriele (1992) to include data collected over nineteen breeding seasons in Hawaii, and conduct a more in-depth analysis. Dates of first and last identification within a given breeding season are assumed to be approximate indices of the relative arrival and departure times of different classes of whale. We investigate whether dates of first and last identification differ between juveniles, females with no calf, females with a calf and males. Moreover, we use a within-subjects design to investigate whether dates of first identification for *individual* females vary as a function of reproductive condition.

## Methods

Photographs of the ventral surfaces of humpback whale tail flukes were collected by staff of the Kewalo Basin Marine Mammal Laboratory (KBMML) between January and April of each year from 1977 through 1995 (see Table 1). The pigmentation patterns and trailing edge of humpback whale tail flukes are unique to individuals (Katona *et al.*, 1979). The whales were photo-identified mainly off the northwest coast of the island of Hawaii (commonly referred to as 'the Big Island') and off west Maui, although some photographs (ca. 1%) were obtained in the waters of Penguin Bank, Niihau and Oahu. Dates of data collection were influenced in large part by the presence or absence of whales each season. Data collection was sometimes suspended at an earlier date off the Big Island than off Maui because whale numbers typically peaked and diminish at an earlier date off the Big Island (Baker & Herman, 1981; Craig, 2001).

The whales were followed in small boats and their tail flukes photographed with a 35-mm camera equipped with a telephoto lens, usually of 300 mm. Most photographs were taken with high-speed black-and-white film, although colour slide film was used on occasion. Whales were typically followed for as many surfacings as were necessary to obtain good quality photographs. There was no deliberate selection of particular pod types for photography.

The best photograph of each whale's tail flukes was assigned a unique observation number and classified into one of five categories according to the degree of white pigmentation. Photographs were then compared visually to all others in the same category. All photographs found to match unambiguously were allocated a common 'resight' number (see Perry *et al.*, 1988). It was thus possible to build a sighting history for each whale identified on multiple occasions.

TABLE 1. *Dates and locations of data collection*

Year	Location	Study period
1977	Maui	12 February - 20 April
1978	Maui	1 February - 8 April
1979	Maui	3 February - 31 March
1980	Maui	27 January - 2 April
	Big Island	15 January - 5 April
1981	Maui	11 January - 12 April
	Big Island	21 January - 24 February
1982	Maui	3 January - 28 March
1983	Maui	1 February - 29 March
1984	Maui	26 January - 28 March
1985	Maui	6 March - 6 April
	Big Island	18 January - 12 March
1986	Maui	1 March - 22 April
	Big Island	19 January - 27 February
1987	Maui	23 January - 12 April
1988	Maui	17 March - 16 April
	Big Island	13 January - 10 March
1989	Big Island	7 January - 3 April
1990	Big Island	11 January - 13 April
1991	Big Island	9 January - 15 April
1992	Big Island	11 January - 3 April
1993	Big Island	15 January - 7 April
1994	Big Island	26 January - 19 March
1995	Big Island	23 January - 19 March

Because the sex of humpback whales is rarely discernible from surface observations, sex was inferred from social role. An adult observed in consistently close proximity to a calf was assumed to be its mother, and therefore female. A whale identified as a singer was assumed to be male, as was any whale identified as an escort to a mother and calf. Molecular sex identification and underwater observations of the genital region have validated these assumptions (Glockner, 1983; Glockner-Ferrari & Ferrari, 1985; Clapham *et al.*, 1992; Medrano *et al.*, 1994). When sex was determined for a whale, it was applied retrospectively to all previous identifications of that individual.

All data associated with each fluke photograph were stored and analysed in SAS (SAS Institute Inc., 1999). Analysis of variance (ANOVA) calculations were performed using the General Linear Model algorithms provided by SAS for the analysis of unbalanced data (Cody & Smith, 1991). An alpha level of 0.05 was used for Tukey HSD *a posteriori* comparisons.

For the purposes of the present study, sightings of individual whales were assigned to one of four categories: male, female with a calf (FC), female with no calf (FNC) and juvenile. Adults of unknown gender were not included in the analyses. Juveniles were perceived by eye by experienced observers to be unambiguously small relative to adults, but too large to be calves-of-the-year. In many cases, these would have been yearling whales that had recently separated from their mothers. It was assumed that females identified without a calf

in a given year did not produce a calf that year, because females are rarely identified both with and without a calf during the same season. For example, a collaborative study using data collected in the North Pacific by eight different research groups over a sixteen year period revealed only four cases in which a female was identified initially without a calf in Hawaii and subsequently with a calf in either Hawaii or Alaska during the same reproductive year (Gabriele *et al.*, 2001). In the present study, these rare exceptions were classed as female with a calf (FC).

Mean dates of first identification were computed for each class of whale from all available data, including whales that were identified on one day only. Mean dates of last identification were computed only for whales identified on more than one day, so that the same data points were not used in both analyses. The within-subjects comparison of date of first identification for individual females as a function of reproductive status included all females that had been photographed as FNCs and FCs in different years. For each of these females, a mean date of first identification was computed for all years in which reproductive status was FNC, and all years in which reproductive status was FC. These mean dates of first identification were then compared for each individual female.

## Results

An ANOVA on the data set combining identifications in all locations revealed a significant effect of location on dates of first identification ( $F_{3,1281} = 10.46$ ,  $p = 0.0001$ ) and last identification ( $F_{3,261} = 4.18$ ,  $p = 0.0065$ ). Consequently, the Big Island and Maui are considered separately.

### *Dates of first identification*

On average, the first whales identified off the Big Island were FNCs, followed by juveniles, males and FCs (Table 2). These differences among classes of whale were significant overall ( $F_{3,650} = 10.14$ ,  $p = 0.0001$ ), and a Tukey test revealed that both juveniles and FNCs were first identified significantly earlier than males and FCs.

Off Maui, the earliest mean date of first identification was for juveniles, followed by FNCs, males and FCs (Table 2). These differences were significant overall ( $F_{3,616} = 8.45$ ,  $p = 0.0001$ ), and a Tukey test revealed that juveniles were first identified significantly earlier than were FNCs, males and FCs.

### *Dates of last identification*

Off the Big Island, FNCs had the earliest mean date of last identification, followed by juveniles, males and FCs (Table 3). There were overall significant differences in date of last identification among classes of whale

TABLE 2. Mean dates of first identification (expressed as day-of-year) for females with no calf (FNC), juveniles, males and females with a calf (FC) off the Big Island and Maui

Class of whale	Big Island			Maui		
	Mean	SD	<i>N</i>	Mean	SD	<i>N</i>
FNC	42.21	17.06	39	60.10	21.30	40
Juvenile	46.66	23.08	44	42.43	18.78	7
Male	56.82	20.50	414	69.99	18.88	421
FC	59.02	21.02	157	71.33	19.17	152

TABLE 3. Mean dates of last identification (expressed as day-of-year) for females with no calf (FNC), juveniles, males and females with a calf (FC) off the Big Island and Maui

Class of whale	Big Island			Maui		
	Mean	SD	<i>N</i>	Mean	SD	<i>N</i>
FNC	43.27	12.34	11	39.00	2.83	2
Juvenile	47.13	17.85	8	–	–	0
Male	65.27	18.84	110	77.00	14.50	68
FC	67.48	19.61	40	76.21	21.30	19

Note: no juveniles were identified more than once within the same year off Maui.

( $F_{3,165} = 7.30$ ,  $p = 0.0001$ ) and Tukey tests revealed that FNCs and juveniles were last identified significantly earlier than males and FCs.

The earliest mean date of last identification off Maui was for FNCs, followed by FCs and males (Table 3). No juvenile was identified on more than one day off Maui. There were overall significant differences in date of last identification among classes of whale ( $F_{2,86} = 5.42$ ,  $p = 0.0061$ ). Tukey tests revealed that FNCs were last identified significantly earlier than males and FCs. Because only a small proportion of FNCs were identified more than once within the same season off Maui, the sample size is small. However, this is consistent with the finding that they are among the first whales to leave the winter grounds, making them less likely to be identified on more than one occasion. Likewise, the finding that no juvenile was identified on more than one day off Maui is consistent with the suggestion that they are among the first whales to leave these waters.

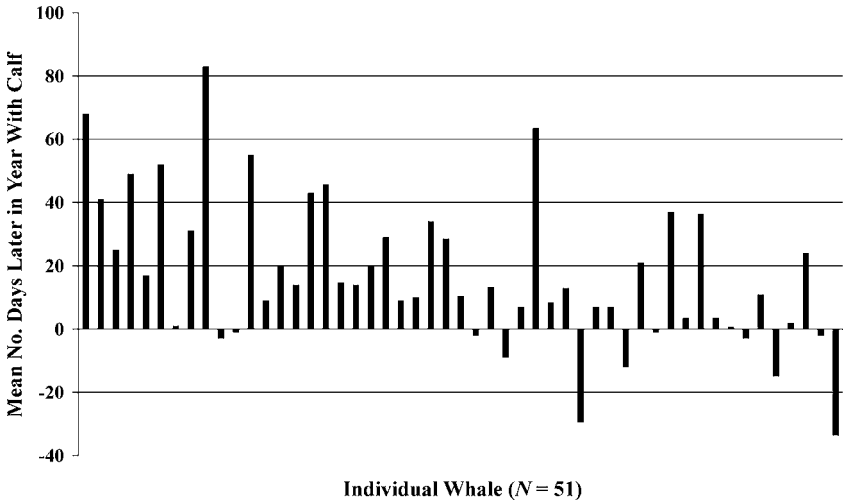


Fig. 1. Individual females: difference between mean date of first identification in years without a calf and mean date of first identification in years with a calf.

*First identifications of individual females as a function of reproductive status*

A total of 51 females were identified as FNCs and FCs in different years. Figure 1 shows that for 40 of these 51 females, the mean date of first identification was later when the female was with a calf than when she was without a calf (sign test,  $p < 0.001$ ). The mean magnitude of this difference was 24.54 days (SD = 20.31) for these 40 females. When all 51 females were considered, the mean difference between mean date of first identification when without a calf and mean date of first identification when with a calf was 17.07 days (SD = 23.58).

**Discussion**

The results suggest that juveniles and females with no calf tend to arrive on and depart from the winter grounds earlier than males and females with a calf, assuming that differences in dates of first and last identification among different classes of whale reflect differences in dates of arrival and departure. Moreover, the migratory timing of *individual* females appears to vary across years, depending on their reproductive status. Females identified both with and without a calf in different years were identified an average of 17

days earlier in the years when they had no calf than in the years during which they gave birth. These findings, based on the individual identification of live whales in Hawaii, corroborate and expand upon those derived from the study of whales caught during commercial whaling operations elsewhere in the North Pacific. As mentioned previously, Nishiwaki (1959, 1966) reported that immature whales tended to migrate to the Ryukyuan Islands at the beginning of the winter breeding season, that immature whales tended to migrate back to the feeding grounds earlier than adults, and that by April, females with calves were predominant in Ryukyuan waters. Although juvenile status was estimated by eye in the present study, the close agreement with Nishiwaki's data suggests that assessments of juvenile status were generally accurate.

Our results are also consistent with the findings of Chittleborough (1965), who analysed catches of humpback whales taken during their migration past the southwest coast of Australia. He found that the first whales to migrate towards the winter grounds were sexually-immature whales and females that were terminating lactation, and the last to migrate were late-pregnant females, with mature males being most abundant in the centre of the migration. He also noted that the classes of whale that were first to arrive in temperate and tropical waters were the first to depart towards the feeding grounds, and that lactating females (who had been in the late stages of pregnancy en route to the winter grounds) were among the last to migrate back to the feeding grounds. Presumably, many of the females with no calf in the sample analysed here correspond to Chittleborough's class of females terminating lactation on the migration route; these females typically weaned their calves as they reached temperate latitudes (Chittleborough, 1965).

Based on the intervals between the mean dates of occurrence for each class of whale at locations ranging from 41 degrees S. (Cook Strait, New Zealand) to 1 degree S. (Congo), Dawbin (1997) concluded that the order of migration to the winter grounds, on average, was as follows: females in late lactation accompanied by weaning yearlings, followed by immature whales 12 days later, mature males 20 days later, resting females 23 days later and late-pregnant females 31 days later. The first whales to commence the return migration were newly-pregnant and resting females together with immature whales, followed by mature males 10 days later and females in early lactation 16 days later. These findings correspond well with our results

with the notable exception of Dawbin's placement of resting females in the midst of the migration to the winter grounds.

Dawbin defined resting females as those whose ovaries and mammary glands showed no signs of recent activity. However, the classification of females as 'resting' may be questionable. Because small embryos were difficult to detect (Chittleborough, 1965; Dawbin, 1966), many of the 'resting' females said to be among the first to migrate from the winter grounds were probably newly-pregnant females. Moreover, we suggest that many of the 'resting' females reported by Dawbin as travelling in the midst of the migration to the winter grounds were in reality newly-pregnant females travelling in the vanguard of the migration back to the summer feeding grounds. The whaling data analysed by Dawbin did not include specific information about the direction of travel of individual humpbacks, and he noted that there may have been mistakes in the designation of migration direction for whales that left the winter grounds early. It is noteworthy that neither Chittleborough (1965) nor Nishiwaki (1959, 1966) included resting females in their descriptions of the temporal sequence of migrating humpbacks. Both considered 'resting' to be a temporary condition preceding ovulation later in the season (Chittleborough, 1954; Nishiwaki, 1959). For example, Nishiwaki (1959, p. 59) noted that some of the ovaries of 'so-called resting' females in the breeding area had much larger Graafian follicles than did those in the feeding area, indicating that they were about to ovulate. Consequently, he considered it more accurate to designate these supposedly resting females as ovulating females in his description of the composition of the humpback whale population in the breeding area.

Our findings are of particular interest in view of the recent report by Stevick *et al.* (2003) that males arrive earlier than females on the West Indies winter grounds. Stevick *et al.* noted the inconsistency between their findings and those of Dawbin (1997), and speculated that different selection pressures may have resulted in different migratory schedules by individuals of the northern and southern hemispheres. Our results suggest otherwise, at least for the North Pacific. Our finding that female migratory timing varies with reproductive state demonstrates the importance of considering these two classes of female separately. If the data for all females are combined, the resultant mean sighting date will depend on the relative numbers of females with and without calves that are present in the data set. Stevick *et al.* reported that even when females with calves were removed from their data

set the difference in migratory timing between males and females remained. Thus, grouping both classes of female together in the analysis is not sufficient to explain the inconsistency between their results and those of both Dawbin (1997) and the present study. Stevick *et al.* found that the sighting dates of humpbacks in the West Indies were earlier for whales migrating from feeding grounds in the USA and Canada than for whales migrating from Greenland, Norway and Iceland. The observed migratory distances ranged from 2300 km to 8080 km. It is possible that these geographical influences on migratory timing masked the effects of sex and reproductive state. Although the influence of feeding ground origin on sighting dates in Hawaii has never been investigated, a recent large-scale study demonstrated an extremely strong migratory link between Hawaii and southeastern Alaska as compared to other feeding areas (Calambokidis *et al.*, 2001). It may be that this dampens any potential effect of geographical influences on migratory timing in Hawaiian waters, allowing the effects of age, sex and reproductive condition to emerge more clearly.

#### *Reasons for variation in migratory timing*

Migratory timing can be seen as a response to the different selection pressures faced by each class of whale. Below, we consider these pressures and the responses of each class of whale.

#### Mature females

Overall, a female's strategy for maximising reproductive success is likely to involve a compromise between the competing demands of (i) encountering and selecting the best possible mate in order to ensure good genetic material for her offspring, and (ii) maximising food intake in order to sustain pregnancy, migration and lactation. Reproduction in general and lactation in particular are energetically costly processes in cetaceans (Lockyer, 1981). The fact that mature female humpbacks are slightly larger than mature males (Matthews, 1937; Nishiwaki, 1959; Chittleborough, 1965; Tomilin, 1967; Spitz *et al.*, 2000) suggests that body size is even more important to female than male reproductive success (Ralls, 1976). Evidence from other mammals indicates that female body weight and condition are related to fecundity (Ralls, 1976; Clutton-Brock *et al.*, 1988). Given the lack of feeding

opportunities on the winter grounds, females are likely to increase their reproductive success by maximising the time spent feeding in high latitudes. The data presented here, indicating that females with no calf appear to be the earliest class of whale to leave the Hawaiian Islands, are consistent with this suggestion. These females presumably commence the return migration to the feeding grounds shortly after conception in order to maximise their food intake before facing the energetic demands of pregnancy and lactation the following year. Indeed, it is possible that some females garner mating opportunities even before their arrival in the winter grounds, and commence migration back to the feeding grounds before reaching the area where mating has traditionally been assumed to occur (Brown & Corkeron, 1995; Craig & Herman, 1997).

As Dawbin (1966) noted, many of the late-lactating females that are first to arrive on the winter grounds are among those that become newly pregnant and are the first to leave for the feeding grounds. After spending the summer feeding in high-latitude waters, these same females (now in the latter stages of pregnancy) are then the last to commence migration to the winter grounds the following winter, presumably because they have been maximising their food intake prior to parturition and the onset of lactation. After females have given birth, their departure for the feeding grounds is probably delayed until such time as their calves are sufficiently robust to have a good chance of surviving the migration to higher latitudes. The present finding that individual females appear to arrive on the winter grounds later in the years when they give birth than they do in the years during which they have no calf fits well with the suggestion that female migratory timing is influenced greatly by the different costs and benefits associated with each stage of the reproductive cycle.

#### Juvenile males and females

The apparent early arrival of juvenile whales in Hawaiian waters probably reflects the large proportion of yearlings that migrate early with their mothers and are weaned either during migration or shortly after arrival on the winter grounds. Our sample of juvenile whales was probably dominated by yearlings because it is relatively easy to distinguish yearlings from other sizes of whale on the winter grounds. Juveniles are unlikely to remain on the winter grounds for extended periods of time. Not only are they physiologically incapable of reproducing, their smaller body size reduces their capacity to accumulate stored energy reserves (Calder, 1984). Thus, juveniles will be less

able than adults to survive prolonged periods without feeding. Further support for the finding that juveniles are likely to exhibit a pattern of early arrival in and departure from the Hawaiian Islands is provided by a videogrammetric study of body size: Spitz (1999) reported that as the breeding season in Hawaii progressed, the proportion of whales that were of sexually immature size decreased.

### Mature males

Because the investment of females in reproduction and parental care is much greater than that of males, females constitute a limiting resource for males (Trivers, 1972). Consequently, males are likely to maximise their reproductive success by competing to inseminate as many females as possible. Both female humpbacks without a calf and those with a calf may ovulate, although conception is less common in the latter case (Matthews, 1937; Chittleborough, 1958; Craig *et al.*, 2002). Although males on the winter grounds exhibit a preference for females without a calf (Craig *et al.*, 2002), the potential for post-partum ovulation means that males will also seek mating opportunities with females accompanied by a calf. Based on the data reported here, the peak presence of females without a calf on the winter grounds occurs early relative to that of females with a calf. Thus, a male seeking to maximise his reproductive success should time his migration such that he overlaps extensively with both classes of female on the winter grounds. This could imply that male arrival should coincide with the arrival of females without a calf, and male departure should coincide with that of females with a calf. However, male residency on the winter grounds is likely to be constrained by the lack of food and consequent requirement to subsist on stored energy reserves. The migratory timing of males reported here and elsewhere suggests that their mating strategies involve a compromise between the benefits of maximising access to both classes of female and the costs of remaining in an environment largely devoid of food resources.

Male-male competition in humpback whales appears to include an element of endurance rivalry (Craig *et al.*, 2002), and its importance as a component of reproductive success in male humpbacks has perhaps been underestimated in the past. The length of time spent on the lek is an important contributor to male reproductive success in species such as the sage grouse (*Centrocercus urophasianus*) (Gibson & Bradbury, 1985) and the fallow deer (*Dama dama*) (Apollonio *et al.*, 1989). Male endurance rivalry also appears

to play a role in the reproductive success of other species in which foraging is either absent or considerably reduced during the breeding season (Andersson, 1994): for example, the northern elephant seal (*Mirounga angustirostris*) (Deutsch *et al.*, 1990), red deer (*Cervus elaphus*) (Pemberton *et al.*, 1992) and harbour seal (*Phoca vitulina*) (Coltman *et al.*, 1997). Based on commercial whaling data, Dawbin (1966) estimated that male humpbacks generally spend approximately 5.5 months on the feeding grounds. The relative importance of male investment in feeding versus searching for mates is probably reflected in the observation that nearly half of the year is spent in each activity.

Because body size is an important determinant of the capacity to store energy reserves (Calder, 1984), smaller male humpbacks are presumably less able than are large males to withstand long periods of residency on the winter grounds. Consequently, the largest, physically fittest males should be better able to exploit the mating opportunities afforded by both classes of female: those who ovulate in the early part of the breeding season and depart at once for the feeding grounds, and those who may ovulate later after giving birth to a calf. It is likely, therefore, that there are differences in migratory timing as a function of male size. Future attempts to examine temporal trends in migration as a function of male size should provide information important to a more complete understanding of the factors that influence reproductive success in male humpback whales.

#### *Proximate explanations of variation in migratory timing*

Temporal trends in migration raise questions about proximate as well as ultimate causation. Nishiwaki (1959) considered that temperature may exert a decisive effect on the migration of humpbacks. However, Dawbin (1966) and Baker (1978) concluded that the rate of temperature change encountered by humpbacks on the feeding grounds is too small to be the factor that initiates migration to the winter grounds. Instead, both proposed that photoperiod is the critical stimulus. Dawbin (1966) went on to suggest that humpbacks in different hormonal states are differentially susceptible to daylength, thus accounting for the finding that migratory timing varies with the sex, maturity and reproductive status of humpback whales. However, a brief consideration of the reproductive physiology of seasonal breeders suggests that the mechanism is not so straightforward. Photoperiod is the most important *zeitgeber*

for most seasonally-breeding mammals including sheep, goats, deer, hamsters, horses and bears (Arendt, 1995; Goldman, 1999; Gerlach & Aurich, 2000). Photoperiodic information is translated via neuroendocrine pathways into hormonal signals that regulate gonadal activity and, in all seasonally-breeding mammals studied thus far, it is the action of photoperiod on the pineal gland that stimulates these physiological changes (Arendt, 1995). The pineal gland of the humpback whale appears to have a typically mammalian structure (Gersh, 1938), and there is no reason to suspect that its function is any different in whales than in other mammals. Thus, Dawbin's suggestion that the sensitivity of humpback whales to photoperiod is influenced by hormonal state is too simplistic, because hormonal state is itself likely to be influenced by photoperiod. Moreover, the annual variability in overall migratory timing that has been observed in both northern and southern hemispheres (Dawbin, 1956; Baker & Herman, 1981; Corkeron *et al.*, 1994) suggests that other factors are involved.

Given the general absence of feeding on the winter grounds (Nishiwaki, 1959; Chittleborough, 1965; Dawbin, 1966), it is possible that the availability of food in high latitudes plays a role in determining if or when whales migrate. Brodie's (1975) suggestion that finding and exploiting a rich food resource could offset the energetic costs of remaining in cold water is supported by observations of humpback whales feeding in southeastern Alaska during the winter (Baker *et al.*, 1985; Straley, 1990). It is also supported by the fact that humpback whales were caught on the feeding grounds of the South Atlantic throughout the winter (Matthews, 1937). There may be a complex interaction between photoperiod, hormonal state, body condition and food availability, with the end result determining when or if individual whales migrate. This question is unlikely to be resolved unless future research incorporates an investigation of the hormonal state of individual whales in relation to photoperiod, prey availability, body condition and the timing of their migration.

#### *Consequences of variation in migratory timing*

The timing of migration in adults has important consequences on humpback whale behaviour on the winter grounds. The temporal segregation of females according to reproductive status accentuates the male-biased operational sex ratio, increasing the number of males that are potentially available to each

female at any given point in time. Thus, females benefit from increased male competition without sacrificing time on the feeding grounds. The unbalanced sex ratio is further intensified by the apparent lack of annual migration to the winter grounds by some females (Brown *et al.*, 1995; Craig & Herman, 1997). Thus, the different migratory behaviour of males and females helps to explain the previously-documented intensity of male-male competition in this species (Tyack & Whitehead, 1983; Baker & Herman, 1984). Moreover, the early departure of females without a calf relative to that of females with a calf also accounts for the finding that there is a significant increase in the probability of males escorting females with a calf in Hawaii as the breeding season progresses (Craig *et al.*, 2002).

Nishiwaki (1959) reported that the sex ratio among humpback whales caught off the Ryukyuan Islands was most biased towards males during March. At this time, presumably, many females without a calf have already left for the feeding grounds but mature males are still present in large numbers. These seasonal changes in operational sex ratio and the temporally-staggered migrations from which they result, together with seasonal trends in reproductive physiology, may account for seasonal trends in pod dynamics and levels of aggression. Based on data collected off Maui, Baker & Herman (1984) reported that the percentage of pods engaged in aggression peaked in early March along with mean pod size and overall abundance. Mobley & Herman (1985) found that the peak rate of pod membership change occurred along with the peak in abundance, again during the first two weeks of March. These observations may appear to suggest a mid-season peak in courtship and conceptions, a suggestion that cannot be refuted by direct observations because copulation has never been observed in this species (Pack *et al.*, 2002). However, the present results suggest that courtship activities centred on females without a calf peak early in the season, whereas those centred on females with a calf peak later in the season. When humpback whale abundance peaks off Maui, many females without a calf will already have mated and commenced migration back to the feeding grounds. The mid-season peak in aggression and overall pod size documented by Baker & Herman (1984) may owe more to the operational sex ratio at this time than to an overall peak in mating and conceptions. Operational sex ratio is known to be a good predictor of the intensity of contest competition for mates in a variety of species (Kvarnemo & Ahnesjö, 1996).

There is additional evidence to support the suggestion that courtship centred on females without calves may peak before overall abundance on the winter grounds. Nishiwaki (1959) suggested that humpback whales caught commercially in the North Pacific commonly gave birth in November, as was suggested by Glockner & Venus (1983) for humpbacks photographed with their calves in Hawaii. Given that the gestation period of humpback whales is 11-12 months (Matthews, 1937; Chittleborough, 1958), these data suggest that conception had occurred early in the breeding season, rather than in mid-season when levels of aggression and abundance are high.

### Conclusions

The timing of migration in humpback whales appears to be inextricably linked to mating strategies and reproductive success. Moreover, knowledge of the migratory timing of different classes of whale does much to enhance our understanding of humpback whale behaviour on the winter grounds. The present finding that the migratory timing of individual females in the North Pacific varies with their reproductive status augments previous work showing that both the habitat preferences and the attractiveness of individual females in this region vary predictably with reproductive status (Craig & Herman, 2000; Craig *et al.*, 2002). Taken together, these studies illustrate the value of conducting investigations at the level of the individual as well as the group, and should prompt future research to do likewise.

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