

Clapham, P.J. 1996. The social and reproductive biology of humpback whales: an ecological perspective. *Mammal Review* 26: 27-49.

THE SOCIAL AND REPRODUCTIVE BIOLOGY OF
HUMPBACK WHALES: AN ECOLOGICAL PERSPECTIVE

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Running head: CLAPHAM - ECOLOGY OF HUMPBACK WHALES

ABSTRACT

Existing knowledge of the social organization, mating system and reproduction of Humpback Whales (*Megaptera novaeangliae*) is reviewed to assess how our current understanding of this wide-ranging marine mammal fits into the predictive framework developed from ecological studies of more accessible terrestrial taxa. The small unstable groups characteristic of this species on its summer feeding grounds appear to be a function of absence of predation and of the patchy, mobile nature of most prey; the absence of territoriality and the minimal importance of kinship in associations are also predictable consequences of the latter. The mating system is similar to both leks and to male dominance polygyny, in which males display (sing) or directly compete (perhaps sometimes in coalitions) for access to females. However, the rigid spatial structure characteristic of classical leks is absent. The mating system of this species is sufficiently different to merit a novel category, and "floating lek" is proposed. The widespread distribution of females resulting from absence of both predation and resources during the breeding season preclude simultaneous monopolization by males of more than one potential mate. Furthermore, these factors, together with a male-biased operational sex ratio, minimize the possibility of competition among females. The intensity of intrasexual competition among males conforms to predictions derived from information on testis size and from expectation of future reproductive success. Female choice and, to a lesser extent, differential allocation of competitive effort by males appears likely. Lack of inter-population variation in social and mating behaviour, and in general reproductive biology, is likely a response to similarity of marine environmental conditions. Year-to-year variation in reproductive rates may be linked to variations in the abundance of prey. The invariably uniparous nature of female Humpback Whales is assumed to be related to the energetic demands of lactation, and the lower ratio of available energy partitioned to reproduction that is characteristic of larger mammals. The reversed sexual size dimorphism of this species may reflect different selective pressures on males and females. Finally, there is now evidence that, as in some other taxa, offspring sex ratio is related to maternal condition.

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INTRODUCTION

Over the past three decades, the twin disciplines of evolutionary and behavioural ecology have clarified much about animal behaviour. Long-term studies of numerous taxa have illuminated the many pressures and imperatives which dictate how animals protect, feed and organize themselves, and the remarkably wide range of strategies with which they attempt to maximize their reproductive success.

For many reasons, such insights into the lives of the larger cetaceans have been difficult to obtain. Even the Humpback Whale (*Megaptera novaeangliae*, Borowski), arguably the most accessible of the great whales, poses formidable challenges to the would-be investigator. Among the widest-ranging of all mammals, the Humpback exists in an environment that is opaque and frequently inhospitable to human observers, and much of its life is spent out of sight beneath the surface of the sea. Until recently, even such a basic factor as the sex of an individual was difficult or impossible to determine. This is unfortunate, since studies of these marine mammals potentially offer an interesting test of hypotheses developed from investigations of terrestrial vertebrates.

Since the development in the mid-1970's of a technique for the identification of individuals (Katona & Whitehead, 1981), considerable effort has been expended on study of free-ranging Humpback Whales in a variety of populations. Long-term studies have accumulated sometimes considerable volumes of data, notably in the North Atlantic and North Pacific (for reviews see Hammond, Mizroch & Donovan, 1990). Here, I review existing knowledge of this species in order to attempt to place what we now know into a broader context. Specifically, some of the ecological factors which influence its reproduction and social organization are considered. I also attempt to assess how current understanding of the social behaviour and mating system of Humpback Whales fits into the general predictive framework developed from studies of more accessible terrestrial taxa. Overall, it is suggested that the characteristics of reproduction and social organization of this species generally conform to predictions derived from ecological principles.

The Humpback Whale

The Humpback Whale is one of approximately 78 extant species in the order Cetacea (whales, dolphins and porpoises). It is a moderately large baleen whale and, as is the case for all mysticetes, females are the larger of the two sexes, with a mean length of approximately 13 metres; males are typically up to a metre shorter (Chittleborough, 1965; Mikhaliyev, 1995).

The species has a cosmopolitan distribution, and is found in all oceans of the world. Like that of most mysticetes, the life cycle is divided into two distinct parts. During the months of spring, summer and autumn, the whales are found in high latitudes, where they feed and where little mating activity takes place (Chittleborough, 1958, 1965; Dawbin, 1966). In late autumn, they undertake a long migration to tropical waters, where the primary activities are mating and calving, and where they are typically found around islands or associated with reef systems (Whitehead, 1981; Whitehead & Moore, 1982). It is clear that Humpback Whales effectively fast during their winter residency in low latitudes; commercial whaling operations found little or no food in the stomachs of whales killed in tropical waters or on the migration back to high latitudes (Chittleborough, 1965; Dawbin, 1966; Lockyer, 1981), and very few observations of

feeding behaviour have been recorded in the breeding range (Baraff *et al.*, 1991). It has generally been thought that the great majority of Humpback Whales undertake this seasonal migration, although Brown *et al.* (1995) have recently challenged this belief. They found a highly male-biased sex ratio among migrating whales off eastern Australia, and suggested that many females do not migrate. Observations from southeastern Alaska (Straley, 1990), the Gulf of Maine (Clapham *et al.*, 1993) and the mid-Atlantic coast of the United States (Swingle *et al.*, 1993) also suggest that some individuals may overwinter in high latitudes, but the extent of this phenomenon remains unclear.

Whaling data have shown that both northward and southward migrations are characterized by a staggering of sexual and maturational classes (Nishiwaki, 1959, 1966; Chittleborough, 1965; Dawbin, 1966): lactating females are among the first to leave the feeding grounds in autumn, followed by immature animals, mature males, "resting" females and lastly by pregnant females. In late winter, this order is broadly reversed, with newly pregnant females among the first to begin the return migration to high latitudes.

The length of the migration varies considerably, both within and between oceanic populations. For example, Humpback Whales from the Gulf of Maine travel some 4600 km to the West Indies and back (Clapham & Mattila, 1988); there, they mix with whales from (among other places) West Greenland, whose return migratory journey will be at least 2000 km longer. In the most extreme case documented to date, individually identified humpbacks feeding off the Antarctic Peninsula have been subsequently recorded off the Pacific coast of Colombia, north of the equator (Stone, Florez-Gonzalez & Katona, 1990), a one-way distance of almost 8000 km. This constitutes a mammalian migration record; it also provides the first direct evidence that whales cross equatorial waters. As noted by Stone *et al.* (1990), this may partly explain recent findings by Baker *et al.* (1990, 1993), who compared mitochondrial DNA haplotypes of Humpback Whales from the North Atlantic and the North Pacific and concluded that the two populations had been in genetic contact more recently than the closure of the Panama Land Bridge. Such long-term gene flow has also been suggested between the Antarctic and the North Atlantic (Palsbøll *et al.*, 1995). However, the seasonal opposition of the hemispheres, and thus of the migratory patterns of Humpback Whales, make it likely that direct contact between austral and boreal populations is infrequent.

Both male and female Humpbacks attain sexual maturity at an average age of approximately five years (Chittleborough, 1965; Clapham, 1992). Females give birth to calves most commonly at intervals of two or three years (Clapham & Mayo, 1990), although post-partum ovulation is common (Chittleborough, 1965) and interbirth intervals of a single year have been recorded (Clapham & Mayo, 1990; Glockner-Ferrari & Ferrari, 1990; Weinrich, Bove & Miller, 1993). Gestation lasts for 11-12 months, and calves are born in tropical waters. Calves begin the process of weaning at about six months, attain independence at the end of their natal year, and typically exhibit loose maternally directed fidelity to specific feeding regions in subsequent years (Clapham & Mayo, 1990; Clapham *et al.*, 1993).

The social organization of Humpback Whales is commonly characterized by small, unstable groups; this is true for both summer feeding areas (Whitehead, 1983; Baker & Herman, 1984a; Weinrich & Kuhlberg, 1991; Clapham, 1993a) and tropical breeding grounds (Herman & Antinaja, 1977; Mobley & Herman, 1985; Mattila *et al.*, 1994). While small groups are the rule, larger assemblages can temporarily form during feeding (D'Vincent, Nilson & Hanna, 1985;

Clapham, 1993a), or in association with aggressive intrasexual competition among males during the breeding season (Tyack & Whitehead, 1982; Baker & Herman, 1984b; Clapham *et al.*, 1992). Furthermore, stable associations, while rare, have been recorded between pairs of whales (Weinrich, 1991; Clapham, 1993a) and even among larger groups (Perry, Baker & Herman, 1990). Juveniles of both sexes become less solitary with age, and by the time they have attained sexual maturity their association patterns are largely indistinguishable from those of adults (Clapham, 1994). Humpbacks exhibit no territoriality on the summer feeding grounds (Clapham, 1993a), and observations of individuals in winter suggest that this is also the case during the breeding season (Tyack, 1981).

Male Humpbacks sing long and complex songs (Payne & McVay, 1971), primarily during the breeding season but also sporadically on the summer feeding grounds (Mattila, Guinee & Mayo, 1987; McSweeney *et al.*, 1989). Whales within a given population sing essentially the same song, and similarities or differences in song structure and content have been used to delineate populations of this species; furthermore, songs progressively change over time (Payne, Tyack & Payne, 1983).

During their summer residency in high latitudes, Humpbacks feed on a variety of small schooling fish, including Capelin, *Mallotus villosus* (Whitehead, 1981, 1983), Herring, *Clupea harengus* (Watkins & Schevill, 1979; Baker *et al.*, 1985), Mackerel, *Scomber scombrus* (Geraci *et al.*, 1989), and Sand Lance, *Ammodytes* spp. (Overholtz & Nicolas, 1979; Payne *et al.*, 1986). In some areas, the primary or exclusive prey are euphausiids of several genera, notably *Euphausia*, *Thysanoëssa* or *Meganyctiphanes* (Matthews, 1937; Nemoto, 1957; Slijper, 1962). Virtually all of a Humpback's potential prey is characterized by patchy distribution, and by variable patch size.

Like all balaenopterids, Humpback Whales are considered "gulp feeders" in that they feed in discrete events, engulfing a single mouthful of prey at a time rather than continuously filtering food in the manner that is characteristic of balaenid whales (Ingebrigtsen, 1929; Watkins & Schevill, 1979). This basic feeding behaviour is often enhanced by the production of bubbles in the form of clouds, nets or curtains to corral or trap prey (Ingebrigtsen, 1929; Hain *et al.*, 1982), a behaviour that is unique to this species. This bubble-feeding technique varies both among individuals and between populations (unpublished data), and it appears to be a learned behaviour (Weinrich, Schilling & Belt, 1992). Humpbacks often forage alone, but are also frequently observed to cooperate in the exploitation of prey (Whitehead, 1983; Baker & Herman, 1984a; D'Vincent *et al.*, 1985).

Finally, while a few attacks on Humpbacks by Killer Whales (*Orcinus orca*) have been observed (Whitehead & Glass, 1985; Florez-Gonzalez, Capella & Rosenbaum 1994), such incidents are extremely rare in most areas where Humpbacks have been studied. Thus it appears that the species does not live under threat of predation over much of its range (Dolphin, 1987). However, the frequency with which tooth marks occur on the flukes and other body parts, particularly in young Humpbacks, suggests that attacks do occur, probably largely on young calves during the migration.

SOCIAL ORGANIZATION

Ecological determinants

As noted by Gosling & Petrie (1981), a social system must be viewed as the summation of the behaviours of the

system's individual members, because it is upon individuals (rather than groups or societies) that selection operates. It is now recognized that the social organization of a population reflects the influence of a variety of ecological effectors and may be further modified by the behaviour of conspecifics; in particular, group size and social behaviour are strongly influenced by predation pressure and the distribution of resources (Clutton-Brock & Harvey, 1977; Gosling & Petrie, 1981; Boesch, 1991).

The formation of a group involves costs and benefits to the individuals concerned. Benefits may include the avoidance of predation (including enhanced predator detection, communal defence or decreased probability of being caught) and greater feeding efficiency (improved location of resources or cooperative capture of prey), as well as increased opportunities for social interactions (mutual parasite removal, establishment of social bonds, or opportunities for courtship of potential mates). The costs of joining or forming a group potentially include increased probability of detection by predators, transmission of disease and increased competition for resources or mates. Benefits or costs may be cumulative; for example, flocking behaviour among birds may permit greater feeding efficiency through a decreased need for vigilance against predators (Lima & Dill, 1990), while competition for mates may leave individuals more vulnerable to predation (Gould & Gould, 1989).

How do these factors influence group formation in Humpback Whales? I have previously (Clapham, 1993a) considered data on school size of certain piscine prey and on the general absence of predation pressure, and suggested that the characteristics of Humpback Whale groups conform to predictions derived from economic theories of social organization such as those summarized by Gosling & Petrie (1981). Specifically, lack of predation obviates the need for permanent large groups, and (as first suggested by Whitehead, 1983) group size appears to be related to prey patch size. The occurrence of many small prey schools will put stable groups of whales at a disadvantage unless they can consistently outcompete others for the best patches.

Intraspecific variations in social structure as a response to quantitative or qualitative differences in prey as well as other ecological factors have been reported in many species (Lott, 1984). From this, one would predict that different patterns of group size and stability would be observed among Humpback Whales feeding on prey possessing characteristics that are substantially different from those reported for *Ammodytes* in the Gulf of Maine. An example may be two consistently large and stable groups of Humpback Whales observed in association with extensive shoals of Herring in southeastern Alaska (Perry *et al.*, 1990), but the absence of quantitative data on prey abundance has precluded confirmation of such a relationship.

The absence of territoriality is also predictable in a species such as the Humpback which subsists on patchy, mobile resources that are unpredictably distributed. The situation with regard to dominance is rather more equivocal. If dominance sorting is generally accompanied by aggressive interactions between individuals (Barnard & Burk, 1979; Clutton-Brock, Guinness & Albon, 1982; Thouless & Guinness, 1986), the virtual absence of observations of such interactions between Humpback Whales on their feeding grounds would suggest that dominance rankings are not established in high latitudes. However, since the abundance of prey must often be limited relative to the number of foraging whales present, some competition for resources should be expected, especially where the same individuals

remain resident in a particular area for a prolonged period. Given that high dominance rank in such situations would presumably increase an individual's fitness, it is somewhat surprising that evidence for such sorting has not been found. That the existing social system evolved before large-scale human exploitation reduced prey stocks, and thus has not developed to accommodate competition, is an interesting but untestable hypothesis. A more likely explanation is that the presumably low encounter rate between specific individuals that results from their wide-ranging movements during a summer makes establishment of a dominance system untenable.

Rôle of kinship

Associations between related individuals form the basis of the social organization of numerous species. Examples include primates (Clutton-Brock & Harvey, 1977), Killer Whales (*Orcinus orca*; Bigg *et al.*, 1990), Scrub Jays (Woelfenden & Fitzpatrick, 1984) and social insects (Wilson, 1975). Related animals may benefit from cooperation by the direct enhancement of their own reproductive success, or by inclusive fitness (Hamilton, 1963, 1964).

Kin-based societies are most likely to develop in situations where related individuals are in close proximity to one another for prolonged periods, and where environmental factors permit many opportunities for cooperative behaviour (Bertram, 1976). A consideration of the ecological factors constraining Humpback Whales suggests that such opportunities may be rare in this species. The disadvantage of stable group formation resulting from the resource characteristics confronting Humpback Whales in at least some areas should apply equally to all animals, whether related or not, unless (as noted above) stable groups can somehow outcompete other whales for access to food. An analysis of the association patterns of individual Humpbacks with known relatives in the Gulf of Maine population found that only four of 2690 pairs consisted of known relatives (Clapham, 1993a), suggesting that kinship plays little rôle in the social organization of Humpback Whales. However, Weinrich (1991) has suggested that stable pairs may be composed of related individuals who would benefit from enhancement of inclusive fitness derived from increased foraging efficiency. In addition, as discussed below, the possibility that related males form coalitions to gain access to females on the breeding grounds (Clapham *et al.*, 1992) cannot be dismissed.

The issue of associations between related individuals in both high- and low-latitude ranges hinges upon a fundamental question concerning the mechanism of kin recognition in a species in which females are uniparous and where weaned young have left their mothers before the birth of a sibling. While phenotypic matching or mother-mediated recognition during feeding ground encounters between a mother-calf pair and the mother's previous offspring are possible mechanisms for kin recognition (Waldman, 1987), it has been argued that reliable data on either are sparse (Grafen, 1990). However, stable groups, although rare, do occur, and molecular studies are required to determine the degree of relatedness of their members. Finally, it is possible that ecological conditions in particular populations of Humpback Whales permit the development of cooperative stable associations between related individuals. The stable groups from southeastern Alaska described by Perry *et al.* (1990) may fall into this category, although recent information suggests that kinship is not the basis for these assemblages (C. Gabrielle, pers.comm.)

Seasonal contrasts, seasonal connections

The marked seasonal contrasts in the life of Humpback Whales have been recognized for many years. The distinct geographic and temporal separation of feeding and breeding in this species is reflected in seasonal differences in endocrinological correlates: females come into oestrus only during the winter, and testosterone levels and sperm production in males show marked peaks at this time (Omura, 1953; Symons and Weston, 1958; Chittleborough, 1965). Similar differences are found in the behaviour of the animal: instances of cooperative feeding behaviour during the summer contrast sharply with aggressive intrasexual competition among males on the winter breeding grounds (Baker & Herman, 1984a, 1984b).

To date, however, little attention has been paid to the possibility that social organization and behaviour in summer can be influenced by that occurring in winter, or vice-versa. This is understandable in view of the paucity of data with which to address such questions, but some consideration of this relationship is merited in view of recent research. First, there is evidence that the frequency of association between mature males in the Gulf of Maine is lower than would be expected by chance. Weinrich & Kuhlberg (1991) interpret this as avoidance and suggest that it represents an extension of intrasexual competition on the breeding grounds. By contrast, I have argued elsewhere (Clapham, 1993a) that associations between males, while disproportionately represented, are far from uncommon; this is particularly true during feeding behaviour, when the costs of assisting a potential competitor might be particularly high. Furthermore, the spatial mixing of whales from different feeding areas on a common breeding range during the winter (Mattila *et al.*, 1989; Katona & Beard, 1990) means that males from the same feeding ground are generally *not* in competition with each other for access to oestrous females. This lack of reproductive competition ensures that there is a low cost to associations between mature males in summer (and potential benefit if such cooperation increases food intake); it may also reinforce the apparent absence of a need for dominance sorting in high latitudes.

Does the high frequency of association between adult males and adult females during the summer, as reported from the Gulf of Maine (Clapham, 1993a) truly reflect a reproductive strategy on the part of one or both sexes? Such associations might permit a male to establish bonds with a large number of females with the possibility of a payoff during the winter. They might also permit assessment by females of males as potential mates. In a similar manner, the occurrence of singing behaviour by males in high latitudes during the summer (Mattila *et al.*, 1987; McSweeney *et al.*, 1989), at a time when Humpback Whales are not mating, may represent low-cost advertisement by males as well as a possible means of assessment of males by females.

THE MATING SYSTEM

Ecological and other influences

Mammalian mating systems show considerable diversity, and include monogamy, polygyny, polygamy and, rarely, polyandry (for reviews see Emlen & Oring, 1977; Clutton-Brock, 1989). Polygyny (of various types) characterizes the majority of studied species in this class, although within a species males and females may employ very different mating strategies. It is now recognized that the spatial and temporal distribution of resources determines a species' mating

system by controlling the distribution of receptive females, and that intraspecific variations in mating behaviour are generally attributable to differences in this distribution between populations or groups (Emlen & Oring, 1977; Ralls, 1977; Lott, 1984; Rubenstein & Wrangham, 1986; Clutton-Brock, 1989). Other factors, such as predation pressure and the behaviour of conspecifics, may modify the system. In general, the more that a resource is economically defensible (usually by males), the more likely a polygamous system of some type is to develop. In Elephant Seals (*Mirounga angustirostris*), for example, the limited availability of suitable pupping beaches results in a clustering of females during the breeding season, thus allowing males to defend large groups of females (LeBoeuf, 1974). As a result, this species is characterized by extreme harem polygyny, with high variance in the reproductive success of males.

How do predictions derived from a knowledge of resource distribution fit with what we now know of the mating system of Humpback Whales? In this context it must first be acknowledged that the annual migration of Humpback Whales from high latitudes into warmer tropical waters exerts a profound influence on the mating system. Explanations of the adaptive advantage of this seasonal migration (which for some whales entails a one-way journey of as much as 8000 km; Stone *et al.*, 1990) remain unproven. The popular intuitive idea that calving in warmer water confers upon neonates a higher chance of survival is given nominal acceptance by many cetologists (e.g. Gaskin, 1982); however, some energeticists find the argument unconvincing, particularly since it fails to explain why whales without calves should also undertake the trip, unless the locomotory costs and prolonged fasting involved in the migration are significantly offset by the thermodynamic advantages of overwintering in warmer water.

Whatever the reason, the consequence of this migration is that, during the period in which Humpback Whales are mating and calving, they occur in areas where prey resources are effectively absent. As a result, females are widely and unpredictably distributed. Furthermore, as appears to be the case in high latitudes, an apparent absence of predation pressure on Humpback Whales in tropical habitats frees individuals from the need to coexist for purposes of communal vigilance or defence, thus reinforcing the tendency for whales to be found alone or in small unstable groups. An analysis of group sizes observed in various parts of the West Indies confirms this, with more than 70% of sightings being of pairs or singletons (Mattila & Clapham, 1989; Mattila *et al.*, 1994); virtually all larger groups are competitive in nature (Clapham *et al.*, 1992; Mattila *et al.*, 1994). The result of this is that male Humpback Whales can defend neither resource-based territories nor groups of females. In other words, although the largest breeding grounds may be host to hundreds of such females, they are never clustered together in such a manner that males can monopolize more than one at a time. As we would predict, therefore, males are found competing for single rather than multiple females (Clapham *et al.*, 1992; Medrano *et al.* 1994; Brown & Corkeron, 1995).

Other predictions follow from a consideration of such a distribution. First, we would expect that intrasexual competition among females should be minimal and may not influence mate selection as it has been shown to do in some species (e.g. Red-Winged Blackbirds, *Agelaius phoeniceus*; Lenington, 1980). Female Humpback Whales may take advantage of the lack of ecological constraints by actively avoiding each other in order to minimize such competition; indeed, a molecular determination of the sex of animals in pairs biopsied in the West Indies in 1992 found no female-female dyads (Mattila, in progress). Aggressive interactions between females have not been reported from any breeding

ground, although the sample size of known females is currently too small to allow us to dismiss this entirely as a possible factor in the mating system. Furthermore, while the operational sex ratio on the breeding grounds is unknown, current evidence on resightings of animals of known sex strongly suggests that it is likely to be skewed towards males (Mattila *et al.*, 1989; Clapham *et al.*, 1992). As noted by Berglund *et al.* (1993), intrasexual competition among females for mates will generally occur only when this ratio is female-biased.

Secondly, as noted by Emlen & Oring (1977), communal displaying behaviour by males is most likely to occur in situations where there is little or no potential for control of resources or mates. Singing by male Humpback Whales is a ubiquitous feature of the winter habitats of this species (Payne & McVay, 1971; Winn & Winn, 1978) and it appears likely that one of its principal functions is as a powerful acoustic display with which to attract potential mates (Winn & Winn, 1978; Tyack, 1981), possibly by providing some indication of the fitness of the singer (Chu & Harcourt, 1986; Chu, 1988). This function has yet to be demonstrated, however; other explanations include a spacing function among males (Darling, 1983), and the synchronization of oestrus in females (Baker & Herman, 1984b).

Thirdly, because ecological conditions (notably resources and temperature) are broadly similar in all of the tropical marine systems in which Humpback Whales occur during the winter, we would expect little intraspecific variation in the mating system between different populations (see Lott, 1984). To date, courtship and competitive behaviour in Humpback Whales have been described in detail from the West Indies (Tyack & Whitehead, 1982; Clapham *et al.*, 1992), Hawaii (Tyack & Whitehead, 1982; Baker & Herman, 1984b; Glockner-Ferrari & Ferrari, 1985; Mobley & Herman, 1985), eastern Australia (Brown & Corkeron 1995), Japan (Darling & Mori 1993), and Mexico (Medrano *et al.* 1994). No qualitative differences have been observed between these major ranges. In addition, singing and competitive groups are frequently observed off Madagascar (P. Folkens, pers. comm.), the Pacific coast of Colombia (H. Rosenbaum, pers. comm.) and western Australia (H. Rosenbaum, pers. comm.).

The one (currently unstudied) Humpback Whale population which is potentially different is that of the Arabian Sea. The recent release of data on large, previously unreported whaling catches by the Soviet Union has been used to make a strong case that this population resides in the region year-round despite the absence of cold high-latitude waters (Mikhailiev, 1995). Local productivity is high and whales of several species have been observed there year-round (see also Reeves, Leatherwood & Papastravrou, 1991). The possibility that Humpbacks can feed in the Arabian Sea during the winter raises interesting questions regarding whether the availability of resources at this time would result in a mating system that is significantly different from that of other populations.

Mobley & Herman (1985) have suggested that the mating system of the Humpback Whale may be characterized as a lek. One of the difficulties with evaluation of this suggestion is that there is some disagreement over exactly what constitutes a lek. Bradbury (1977, 1981) discusses this problem and provides both primary and secondary criteria including absence of parental care, existence of a mating arena, lack of resources in male territories, and opportunity for females to select males; leks involve epigamic displays by males, who also exhibit highly skewed mating success. Wilson (1975) employs rather broader criteria, and does not exclude species for whom "lek" territories contain resources such

as food. The Mobley & Herman (1985) hypothesis is superficially attractive because of the presence of many singing (i.e. possibly displaying) male Humpback Whales in an area during the mating season; furthermore, it fulfills a prediction made by Emlen & Oring (1977) that leks should arise where resources are economically indefensible (in this case, absent). However, the hypothesis ignores one of the principal features of a classical lek which is the establishment by males of territories, as well as the observation that territories in the centre of the lek are generally occupied by high-ranking males who enjoy high mating success (Emlen & Oring, 1977; Wiley, 1978; Bradbury & Gibson, 1983). While the existence of all-male competitive groups (Clapham *et al.*, 1992) may suggest the establishment of dominance rankings among males who are temporarily resident in a specific area, observed movements of individually identified males around and between such areas (Baker & Herman, 1981; Mattila & Clapham, 1989; Mattila *et al.*, 1989, 1994) indicate that rigid spatial structuring of the type observed in lek territories does not occur in this species.

If Humpback Whales are not reliant on specific resources in tropical waters, and if their mating system is not a lek (at least not as currently defined; but see below), why then do they congregate in certain areas of the breeding range, sometimes in large numbers? On Silver Bank in the West Indies, for example, as many as three thousand whales may be present at the peak of the season (Winn, Edel & Taruski, 1975; Balcomb & Nichols, 1982; Mattila *et al.*, 1989). It is possible that the apparent requirement of mothers with newborn calves for sheltered water on the leeward side of islands or reefs (Whitehead, 1981) may partly explain the aggregations of whales that occur in such areas, although there is no obvious reason why other classes of whales should be similarly confined in their distribution. Indeed, the fact that relatively few females calve in consecutive years (Baker, Perry & Herman, 1987; Clapham & Mayo, 1987, 1990; Glockner-Ferrari & Ferrari, 1990) indicates that the majority of mated females are not lactating. It is possible that the clustering of Humpback Whales in specific tropical habitats during the winter facilitates mate selection by both sexes in the manner which has been proposed for other species (Alexander, 1975; Emlen & Oring, 1977; Parker, 1978), but this question cannot be addressed without data on the differential mating success of whales within and outside such areas.

From current knowledge it appears that the mating system of the Humpback Whale does not easily fit into a recognized category. This is perhaps not surprising, given that existing terms have largely been derived from research on terrestrial taxa; there has been little consideration of the different constraints and opportunities presented to marine species whose courtship behaviour must be conducted in three dimensions. The Humpback's mating system is most similar to what Emlen & Oring (1977) describe as male dominance polygyny. Humpback Whales appear to fulfill most of the requirements of a system of this type: that economic defence of either resources or multiple females is impossible, that male parental care is absent, that communal display behaviour by males occurs, and that males engage in direct competition for access to oestrous females. With the possible exceptions of the all-male groups described from the West Indies (Clapham *et al.*, 1992), and of occasional apparently aggressive interactions between singers and conspecifics (Tyack, 1981; Darling, 1983), dominance sorting among male Humpback Whales has yet to be documented; this is discussed further below. In summary, the mating system of this species incorporates most of the elements of male dominance polygyny and all of the characteristics of a classical lek except for rigid spatial structuring. It seems that a novel term is merited. I would suggest that "floating lek" (no pun intended) succinctly captures the features of this

system, including the movement of displaying males.

Irrespective of which term is applied, the issue of male dominance must be resolved. That some degree of such sorting would occur seems reasonable in light of the apparent residence characteristics of males documented in some locations (Clapham *et al.*, 1992), as well as the reduced costs associated with prior assessment of the likely outcome of interactions. If, as suggested by Chu & Harcourt (1986) and Chu (1988), females can assess the condition of individual males based upon some cue in their song, presumably males could also assess other males in the same manner, as has been reported for red deer (Clutton-Brock & Albon, 1979), hammer-headed bats (*Hypsignathus monstrosus*; Bradbury, 1977) and toads (*Bufo bufo*; Davies & Halliday, 1978). The occurrence in the same wintering area and often in the same competitive groups of individuals of different high-latitude origins (Mattila *et al.*, 1989; Katona & Beard, 1990; Clapham, Mattila & Palsbøll, 1993) means that most intrasexual competition for mates will occur among unfamiliar conspecifics who will have had no opportunity to establish dominance rankings prior to arrival. Furthermore, the lack of previously established dominance rankings among many males would explain the frequency with which aggressive interactions occur. As discussed below, however, these interactions rarely if ever pose a serious threat to the health or life of a combatant.

Finally, as noted elsewhere (Clapham, 1994), it appears that the social behaviour of individual Humpback Whales develops in a similar way to that documented for other mammals, with the attainment of sexual maturity representing a critical time at which both males and females take on adult rôles. Furthermore, observations of individuals of known age (Clapham, 1992) suggest that, as is the case for many species with polygynous mating systems, males may be recruited into the breeding population somewhat later than females (Greenwood, 1980; Johnson, 1986).

Expectation of future reproductive success and the intensity of male-male competition

An individual's lifetime reproductive success can be defined as the number of surviving and breeding offspring it leaves during its life. In many species, low life expectancy and other factors result in an individual's lifetime reproductive success being concentrated into very few or even single mating attempts (e.g. some social insects and arachnids, Thornhill & Alcock, 1983). By contrast, in long-lived mammals lifetime reproductive success is usually distributed across many breeding seasons. For animals in both categories, a single mating opportunity can be viewed in terms of the value of that opportunity relative to expected future reproductive success. If an animal's entire lifetime reproductive success is concentrated into a single mating opportunity, its expected future reproductive success at the time of that opportunity will be zero. For an animal with a life expectancy of years or even decades, however, the value of a current mating opportunity will constitute only a small proportion of its lifetime reproductive success; consequently, its total expected future reproductive success will be higher than that of the present, unless the individual is approaching the end of its reproductively active life.

This situation has many ramifications for the reproductive behaviour of an individual. As noted by Enquist and Leimar (1990), one consequence of the balance between the value of current and expected future opportunities is that fatal

fighting will generally occur only when a large part of a contestant's lifetime reproductive success is at stake. By contrast, serious fights rarely occur between individuals for whom the combined value of future opportunities greatly exceeds that of the present.

Because of the long life expectancy of Humpback Whales (which may exceed that of some of the biologists studying them!) and the difficulties inherent in the study of these animals, no quantitative data exist concerning the lifetime reproductive success of individuals of this species. However, it is obvious that the lifetime reproductive success of both males and females must be spread over many breeding seasons. Observations of individual male Humpback Whales in many competitive groups, sometimes in more than one winter (Clapham *et al.*, 1992) strongly suggest that males will attempt to mate with many females during a breeding season, and many more over the course of their lifetime. Consequently, the future expected reproductive success of a male Humpback Whale will almost always exceed that of a specific opportunity that might follow the defeat of other males in a competitive group. As would be predicted by Enquist and Leimar (1990), while fights between males of this species are occasionally spectacular because of the sheer size and power of the contestants, they appear not to involve serious injury or death. Although open bloody wounds are commonly seen in members of competitive groups (Baker & Herman, 1984b; Mattila *et al.*, 1989), particularly on protruding features of the whale such as the dorsal fin and tubercles, and blood is frequently observed on the caudal peduncle, more serious injuries have yet to be recorded.

Competitive groups: mate guarding and the duration of oestrus

The general structure of Humpback Whale competitive groups was first elucidated by Tyack & Whitehead (1982), who noted that they typically contain a central, relatively passive "Nuclear Animal", and a "Principal Escort" who maintains position next to the Nuclear Animal and frequently fends off challenges to this position from one or more other whales. Molecular determination of the sex of participants of such groups in the West Indies and off eastern Australia has confirmed that Nuclear Animals are generally female, and that all other participants in the groups are male (Clapham *et al.*, 1992; Brown & Corkeron, 1995). However, while none of the studied groups in either location contained more than one female, some consisted entirely of males, a situation which Clapham *et al.* (1992) tentatively interpreted as dominance sorting. There is also evidence from both studies that males may pair up to form a coalition in efforts to displace a Principal Escort.

A central question with regard to competitive groups is whether the Principal Escort is competing for a female in the hope of subsequently mating with her, or is practising the post-copulatory mate guarding behaviour (to prevent other males from mating) that is common in many species (e.g. Magpies, *Pica pica*; Birkhead, 1979). Given the parallels between competitive groups and tending behaviour in ungulates, where a male will associate with an oestrous or pro-oestrous female until he either copulates with her or is displaced by another male (Hafez & Schien, 1962; Leuthold, 1977; Sinclair, 1977), it seems likely that both situations are involved. In this context, the principal item of missing information concerns the duration of oestrus in female Humpback Whales. Regrettably, no data of this type exist, either for this species or for any other mysticete. The duration of oestrus in other mammals varies considerably, from less than an hour

in some rodents, as little as a few hours in red deer (Clutton-Brock *et al.*, 1982) to eight or nine days in dogs and horses (Marler & Hamilton, 1966). Our recent study of competitive groups in the West Indies (Clapham *et al.*, 1992) recorded no resightings of pairs consisting of a previously identified Principal Escort and Nuclear Animal, suggesting that female Humpback Whales begin the return migration to high latitudes shortly after the initiation of pregnancy, a belief which fits well with the early departure of such females documented from whaling data (Chittleborough, 1965; Dawbin, 1966). However, data gathered on Silver Bank in 1992 yielded resightings of several identified Nuclear Animals over periods of between 24 hours and three weeks (Mattila & Clapham, pers. obs.). In one case, a female was escorted by the same male on two consecutive days. These new data suggest either that oestrus lasts for several days or longer in Humpback Whales (requiring prolonged mate-guarding behaviour by males), or that, as in ungulates, males associate with females during a pro-oestrous period. The longer resighting intervals may represent females who were polyoestrous but who failed to conceive during their first cycle.

How males might detect oestrus or pro-oestrus in females is unknown. Female Humpback Whales may advertize their oestrous state, as do African Elephants (*Loxodonta africana*; Poole *et al.*, 1988); this is perhaps suggested by occasional observations of competitive groups forming around female Humpback Whales who are lobtailing or flippering, behaviours which are probably audible underwater over some distance. Alternatively, there may be physiological or postural correlates of this condition, as occurs in many species (e.g. Bison, *Bison bison bison*: McHugh, 1958; domestic cattle, *Bos taurus*; French *et al.*, 1989).

It is worth noting that, despite literally thousands of hours of observations made by biologists over many years in the West Indies, Hawaii and elsewhere, actual copulation in Humpback Whales has yet to be observed. Copulation at the surface has been reported in both Southern and Northern Right Whales (*Eubalaena australis* and *E. glacialis*, respectively; Payne & Dorsey, 1983; Kraus, 1986), and in Grey Whales (*Eschrichtius robustus*; Swartz, 1986); presumably the Humpback Whale copulates exclusively underwater. Copulation may be rapid (Slijper, 1962), as it is in most ungulates (Clutton-Brock *et al.*, 1982). While there is little doubt concerning the intent of males in competitive groups, final confirmation of mating between the Nuclear Animal and her consorts awaits the use of molecular techniques with which to determine paternity.

Males and females: different rôles, different strategies

As has been shown in many species (Rubenstein, 1980; Dunbar, 1981), we should expect variation in mating strategies in Humpback Whales, both within and between sexes, although current evidence for the existence of such variation is rather scant. Chu & Nieukirk (1988) noted the often very different degrees of dorsal fin scarring (presumably resulting from bodily contact during intrasexual competition) among Humpback Whales in competitive groups. They suggested that not all males had an equal probability of attaining Principal Escort status within such groups. This is a logical hypothesis given that size and stamina are probably major determinants of success in such situations, as they are in many other taxa (e.g. LeBoeuf, 1974; Clutton-Brock *et al.*, 1982). Males who are unable to successfully compete by direct conflict may display (sing) to attract females, perhaps in combination with a "roving male" strategy by which they

colonize low-density habitats, where there will be fewer mates but also fewer competitors; as noted by Davies & Halliday (1978) from a study of toads, this strategy is often as successful for a smaller or low-ranking male as searching for a mate in high-density areas. This might explain the occurrence of singing male Humpback Whales in areas of the West Indies where few Humpback Whales are found relative to the major known habitats in Dominican waters (see Mattila & Clapham, 1989).

The rôle of song, and its relative efficacy as a mating strategy, is a critical issue in the behavioural biology of Humpback Whales. Parallels with many taxa strongly suggest that it is indeed a male display designed to attract females, and recent observations by Medrano *et al.* (1994) of females joining singers support this belief. That it also functions as a mechanism which mediates interactions among conspecifics, particularly males, appears highly probable. Playback experiments (Tyack, 1983; Mobley, Herman & Frankel, 1988) have suggested this, and Frankel (1994) has shown that the distribution of singers in Hawaii is both relatively even and density-dependent. But is singing secondary to directly competing for females? Tyack (1981) pointed out that the presumed peak of oestrus (calculated from whaling data) coincides with the shortest song bouts of the winter. This period is exactly the time in which we would expect males to interrupt singing to pursue females, as well as to engage in agonistic interactions with other males. However, as noted above, not all males may be sufficiently large or fit to successfully engage in such competition.

The occurrence of apparently cooperative male-male pairs in competitive groups could be taken as evidence that males who are unable to successfully displace a Principal Escort alone may adopt coalition formation as an alternative strategy. As noted elsewhere (Clapham *et al.*, 1992), it is difficult to see the benefit of such a strategy to both coalition partners unless one assumes that the males concerned are related; coalitions of the latter type may result in benefits to a non-mating male through inclusive fitness (Hamilton, 1964; Wilson, 1975; Hughes, 1986). Coalitions need not be made up of kin, but as a recent molecular-based study of lions has shown (Packer *et al.*, 1991), coalitions composed of unrelated males remain together only if all members father at least one offspring; by contrast, kin-based coalitions are sometimes larger and may involve no successful paternity on the part of low-ranking members.

Escorts to mother/calf pairs on the breeding grounds are invariably male (Glockner-Ferrari & Ferrari, 1985; Medrano *et al.*, 1994), and it has been suggested by Darling, Gibson & Silber (1983) that escorts associate with lactating females in the hope of mating them if they come into post-partum oestrus. However, the high cost of lactation (Lockyer, 1987) makes it likely that a female who is simultaneously pregnant and lactating will be in poorer body condition during the year in which she is nursing the subsequent calf. The percentage of females that we have observed (Clapham & Mayo, 1990) with consecutive-year calves in the Gulf of Maine (a feeding area) was significantly lower than that recorded by Glockner-Ferrari & Ferrari (1985) from the Hawaiian breeding grounds. If this is not entirely due to a bias in sampling towards mothers off Hawaii, the difference may at least partly reflect higher mortality among second calves (those born after an interval of one year) prior to arrival in high latitudes. If this is indeed the case, then escorting a mother/calf pair on the breeding grounds may be a strategy that is inferior to courting or competing for a female who is not currently incurring the expense of lactation. A prediction that should be tested with future research is that individuals observed as lone escorts to mother/calf pairs should have a low probability of being observed as Principal Escorts in competitive

groups that do not contain a calf; data presented by Chu & Niekirk (1988) on scarification of presumed males have implied that this may be the case. Furthermore, I predict that forthcoming genetic studies will find significantly lower rates of reproductive success on the part of such whales, both individually and as a class.

Fisher (1958) stated that both males and females should be expected to discriminate among potential mates if such choice was likely to affect reproductive success. However, as noted by Wasser (1983) and others, the rôle of females in mammalian mating systems has until recently been given less attention than that of males, whose behaviour (such as fighting) is often easier to observe and interpret. It is now widely accepted that females exercise choice over mates and may even compete for them in situations where the operational sex ratio is skewed towards females (Berglund *et al.*, 1993). In a species such as the Humpback Whale, in which male parental investment is absent and the costs of reproduction to females may be considerable, it seems reasonable to assume that females exercise some choice based upon suitable criteria for the acceptability of a potential mate. In other taxa, such criteria are generally assumed to involve heritable qualities such as size and competitive ability that may confer higher reproductive success on offspring (Gosling & Petrie, 1981). The discovery of apparently aggressive females (two animals wrongly labelled as Principal Escorts because of their agonistic behaviour) in competitive groups (Clapham *et al.*, 1992) may represent the repulsion of one or more unsuitable males; this seems particularly likely in light of the fact that one of the males concerned was a known subadult. Flight from, or repulsion of, the advances of males by oestrous females has been documented in other species, as has female solicitation of challenges to tending subadult males from larger, older males (e.g. Elephant Seals: Cox & LeBoeuf, 1977; African Elephants: Moss, 1983; Poole, 1989). Such challenges potentially provide females with a means to assess mate quality. No data exist to address the question of whether female Humpback Whales incite the displacement of younger males by older males, although Glockner-Ferrari & Ferrari (1985) have witnessed what they have interpreted as attempts by females in competitive groups to influence the choice of an escort. In light of the acoustic transmission properties of water, we should not be surprised to find that female Humpback Whales acoustically solicit the formation of competitive groups in a manner similar to that shown for other mammals.

How females might assess males cannot currently be determined, although for reasons noted above, the acquisition of a territory containing resources of value to the female (a common criterion for mate selection among mammals and birds; see Davies, 1978) can be ruled out in this species. Assessment of males (if it occurs) must be based upon other criteria. Size, endurance and fighting ability in competitive groups is one obvious possibility. Chu & Harcourt (1986) and Chu (1988) have also suggested that Humpback Whale song may contain some cue to the fitness of the singer, notably diving ability as indicated by song length (although one could argue the opposite case, that females might favour short songs because these may reflect a *faster* display rate in a given period of time, a criterion which is correlated with high mating success in several lekking species (e.g. sage grouse: Wiley, 1978)). However, it is difficult to reconcile this idea with the fact that mean song length within a population varies considerably between years (Payne *et al.*, 1983).

It has often been assumed that males will mate with any available female (e.g. Wittenberger, 1979), although male choice of females by reproductive potential has been strongly suggested for bison (Berger, 1989), and possibly for some primates (Anderson, 1986). It is curious that, while lactating females are often at the centre of competitive groups in

Hawaiian waters (Baker & Herman, 1984b; Glockner-Ferrari & Ferrari, 1990), their occurrence in such groups in the West Indies is far less frequent (Clapham *et al.*, 1992). The absence of calves from most competitive groups in the latter region may reflect a preference by males for females who are not lactating (and are therefore in superior condition). However, why such a phenomenon should apparently not also be observed elsewhere is difficult to understand unless the frequency of post-partum oestrus differs between populations. Current data on Humpback Whales do not bear on this question, but it should be noted that, in light of the costs to males of intrasexual fighting over several weeks or months (during which no feeding takes place), differential allocation of competitive effort based upon female condition is not unlikely.

An anecdotal observation is worth noting in this regard. Data gathered from Silver Bank in the West Indies in the winter of 1992 yielded resightings of what appeared to all observers to be a very large female Humpback Whale in three competitive groups over a period of three weeks. What makes this observation of interest is that the groups in which the female concerned was the Nuclear Animal were the three largest among more than sixty competitive groups observed that winter, with sizes which ranged from a minimum of thirteen animals to a maximum of more than twenty (the modal size of competitive groups is three; Clapham *et al.*, 1992); indeed, these were some of the largest groups ever recorded in the West Indies. Can the apparently considerable attractiveness of this large female be taken as an indication of a preference by males for a potential mate in superior condition? It is of course not possible to say, but the occurrence of the same individual in groups of such consistently large size suggests that it may.

A final point in consideration of the mating system of Humpback Whales relates to the possibility of sperm competition in this species. This phenomenon, which involves the dilution or displacement of the sperm of another male, was described in insects by Parker (1970) and subsequently for primates by Harcourt *et al.* (1981); it has since been suggested for a wide variety of taxa. A general prediction of sperm competition theory is that species in which the testes of males are large relative to body weight should be expected to engage in sperm competition and be characterized by polygamy among females. By contrast, males of species with small testes are more likely to engage in competition at the individual level (i.e. through direct aggressive interactions). In baleen whales, there is considerable variation in relative testis weight between species: male right whales, which weigh up to 50 tons, possess testes whose average weight is 972 kg each (Omura *et al.*, 1969), the largest in the animal kingdom, while those of the blue whale (a species with a maximum weight in males exceeding 100 tons) have a mean weight of only 70 kg (Ohno & Fujino, 1952). Male Humpback Whales (maximum weight approximately 40 tons) have relatively small testes for their body size (mean = 38 kg: Nishiwaki, 1959); consequently, the occurrence between individual males of aggressive interactions of the type that occurs in competitive groups is to be expected (Brownell & Ralls, 1986).

REPRODUCTION

Ecological influences on reproductive rates

Virtually nothing is known of the environmental factors governing Humpback Whale reproduction or associated behaviours. For example, while Dawbin (1966) considered various factors which might act as migratory cues, a

connection between a specific seasonal predictor and migration remains undemonstrated, and our understanding of the neuro-endocrinological pathways that underlie such behaviour in this species is effectively nil. Many factors are known to influence reproduction in large mammals; these include sex, life expectancy, body size, diet and thermodynamics. It is safe to assume that the reproductive histories of Humpback Whales can likewise be viewed as the end result of complex interactions between these and other variables; yet beyond such generalizations, little is known of the specific rôles played by such factors. Even within the more accessible terrestrial taxa, investigations of this type have often been focussed on species living in temperate latitudes, and many have ignored or minimized the very different selective pressures operating on males and females (Bronson, 1985).

Many terrestrial mammal species exhibit considerable variation in the timing and duration of reproduction, between and sometimes within populations (Brown, 1945; Lee, 1970), principally in response to climatic variables. By contrast, the reproductive cycle of Humpback Whales appears to be the same across all studied populations (Dawbin, 1966). Such uniformity is presumably associated with the more predictable and less variable temperature regime of the marine environment (notably that of the tropics), combined with the thermodynamic advantages of large size.

As shown in recent studies, however (Baker *et al.*, 1987,; Clapham & Mayo, 1987, 1990), Humpback Whales do show year-to-year variation in reproductive rates, albeit considerably less marked than in species which are more vulnerable to acute environmental changes. The principal factor determining inter-year variations in reproductive rates of Humpback Whales may be the availability of food. To date, no studies of this nature have been conducted, although unpublished data from Prince William Sound in Alaska show a correlation between local abundance of prey and the following year's crude birth rate (Dolphin, 1985). A similar correlation has been observed in the Gulf of Maine (Clapham, 1993b).

As discussed above, the difference between current and expected future breeding opportunities may influence reproductive behaviour (such as the intensity of contests) in males. Among females, possible tradeoffs between present and future opportunities are less obviously manifest. Female Humpback Whales produce calves regularly at two- or three-year intervals (Baker *et al.*, 1987; Clapham & Mayo, 1987, 1990), probably throughout their reproductive life. Thus, as with males, the lifetime reproductive success of females is spread over many years. Dolphin (1985) speculates that a female Humpback Whale who is pregnant in a year characterized by poor prey resources should, through spontaneous abortion, defer reproduction because the value of reproduction in a future year when food is more abundant will be greater than that in the present (a general principle which is discussed in detail by Krebs and Davies, 1987). It is impossible to determine whether apparent positive correlations between availability of food and the crude birth rate of Humpback Whales in the area the following year reflect the occurrence of spontaneous abortion during poor food years, since no data relating to this phenomenon exist for Humpback Whales.

The influence of body size

In recent years, the importance of body size in considerations of the life history of an animal has been widely

recognized. Western (1979) reviewed available data and concluded that gestation, growth rate, age at sexual maturity, life expectancy, birth rates and degree of parental investment are all allometrically scaled to body size across a broad range of taxa. Others (e.g. Ralls, 1976) have attempted to understand the proximate and ultimate factors responsible for the phenomenon of sexual size dimorphism within species. Humpback Whales are among the largest animals on Earth, with adult body weights that may exceed 40,000 kg. As is the case for all mysticetes, females are the larger of the two sexes (Ohsumi, 1966).

For the most part, we can draw only broad inferences regarding the effect that the Humpback's large size has on its biology. Some of these are obvious: home range, for example, is very large. In addition, Humpback Whales are invariably uniparous (Baker *et al.*, 1987; Clapham & Mayo, 1987). Furthermore, whaling catch data show that very few Humpback Whale pregnancies (0.39%, Slijper, 1962; 0.28%, Chittleborough, 1965) involve multiple fetuses. This conforms to a general tendency for litter size to decline with increasing body size, which in turn is related to the fact that the proportion of available energy that can be partitioned to reproduction decreases with the size of the animal (Fenchel, 1974). This may be especially true for cetaceans, in which the energetic costs of producing a fat-rich milk are particularly high (Lockyer, 1987), thus diminishing the possible viability of multiple calves (in Humpback Whales, the fat content of the milk is approximately 32-38%: Pedersen, 1952).

The question of why females mysticetes should be larger than males was considered by Ralls (1976), who concluded that, as in other mammalian species in which females are the larger of the two sexes, this "reversed" sexual size dimorphism can generally be explained by the principle that larger females are more efficient mothers (Thomson, 1959). Specifically, they may better be able to offset the energetic costs associated with rapid foetal growth and lactation, notably since much of their year is spent in cold water. If this is true, one might expect a smaller degree of reversed sexual size dimorphism among Bryde's Whales (*Balaenoptera edeni*), which remain in the warm waters of low latitudes all year. Unfortunately, existing data on the comparative lengths of males and females of this species are insufficient to test this prediction.

A parallel principle, first advanced by Darwin (1871), that sexual selection acts to favour large size among males in species in which males engage in combat for access to females, might be considered paradoxical in a species such as the Humpback in which such combat occurs but where females are on average larger than males. Few data exist with which to address this question; however, that female Humpback Whales are bigger than males is not necessarily incompatible with the idea that sexual selection favours large size in the latter sex. The relative sizes of the two sexes may be the product of two very different selective forces, with the bioenergetic constraints on lactation favouring larger size in females to a greater degree than does competitive ability among males. Furthermore, while male Humpback Whales do fight, it is clear that they invariably compete for single rather than multiple females (Clapham *et al.*, 1992). In this respect, it is noteworthy that it is in species characterized by harem polygyny that the most dramatic examples of sexual size dimorphism are found (e.g. Elephant Seals: LeBoeuf, 1974).

Adaptive variation in sex ratio of offspring

The Trivers & Willard (1973) hypothesis states that the "ability" of female mammals to vary the sex ratio of their

offspring should be selected for in those species where there is a greater variance in reproductive success among members of one sex (generally males), and where the body condition of the mother during the period of parental investment affects the future condition (and competitive abilities) of the offspring. Since the publication of this controversial hypothesis, numerous studies have attempted to correlate maternal condition or maternal investment with the sex ratio of offspring. Results have been mixed. Examples which have contradicted the hypothesis include studies of White-tailed Deer (*Odocoileus virginianus*: Verme, 1985), Reindeer (*Rangifer tarandus*: Skogland, 1986), and American Bison (Green & Rothstein, 1991). Evidence in support of Trivers & Willard (1973) has come from studies of Red Deer (Clutton-Brock, Albon & Guinness, 1986), American Bison (Rutberg, 1986), Caribou (Thomas, Barry & Kiliaan, 1989), Suffolk sheep (Kent, 1992), and humans (Mueller, 1993). Recently, Wiley & Clapham (1993) provided data suggesting a correlation between maternal condition and offspring sex ratio among Gulf of Maine Humpback Whales. Specifically, mature females on longer interbirth intervals were significantly more likely to produce sons. The authors suggested that such females were likely to be in better condition, having less recently incurred the costs of lactation.

As with much in biology, it is unlikely that observed sex ratios among mammals are the result of consistent and simple cause-effect relationships. Single correlates of offspring sex ratio other than maternal condition have been suggested, including maternal stress, population demographics, mother's dominance rank, mother's age, and habitat quality. Clutton-Brock & Iason (1986) provided a comprehensive review of existing studies of sex ratio variation and concluded that their results did not conform to the predictions of any single adaptive hypothesis.

Theoretical clarity on this issue, and a more viable general model of sex ratio variation, is provided by Armitage (1987), who suggests that attempting to correlate sex ratio variation with any single factor is a classic example of misplaced emphasis. Rather, investigators should focus on the consequences (i.e. reproductive success) of sex ratio variation, not the cause (e.g. maternal condition), because it is the former, not the latter, on which selection acts. Armitage summarized data on yellow-bellied marmots in addition to reviewing information on other taxa and concluded that females produce the sex with the higher probability of reproductive success, irrespective of the costs associated with the production of that sex, and that the bias towards one sex or the other will vary with current social and environmental conditions.

To date, no unequivocal evidence has been presented in support of a possible mechanism for the determination of sex, although James (1986, 1989) has suggested that parental levels of several hormones (including gonadotrophin, oestrogen, testosterone and progesterone), affect the sex of mammalian offspring. As suggested by Armitage (1987), it appears likely that natural selection maintains the physiological variability (whatever this is) that can respond to the many proximal factors that cause biased sex ratios.

Unfortunately, the manner in which these various factors may affect birth sex ratios in Humpback Whales is not determinable on the basis of existing information. The skew towards males in the Wiley & Clapham (1993) study was among the strongest found for any mammal, yet the overall sex ratio in the population concerned is at parity, both overall and among different age classes (Clapham, Bérubé & Mattila, 1995). This presents a paradox, since a biased ratio towards males should result in a similar bias in the overall population. At this point we can say only that a bias exists, and further research is required.

CONCLUSIONS AND FUTURE PROSPECTS

While a great deal remains to be learned about the Humpback Whale, it is becoming clear that, contrary to the many romantic public perceptions of this species, it is essentially no different from any other mammal in the way that it confronts and exploits the various problems and opportunities presented by its ecology. Given a knowledge of the Humpback Whale's habitat, prey characteristics and predation pressures, the reproduction, social organization and mating system of this species appear to conform well to predictions derived from the general ecological principles that govern the behaviour and evolution of other taxa.

While the continuation of long-term studies will undoubtedly yield further insights into the biology and behaviour of Humpback Whales, it is clear that new approaches are required to elucidate many remaining issues. Molecular techniques will undoubtedly provide a significant new means with which to address certain questions; in particular, microsatellite markers (recently employed with considerable success by Amos, Schlötterer & Tautz (1993) in a study of pilot whales, *Globicephala melaena*) promise to provide quantitative data on social organization and reproductive success. In addition, satellite radio tagging, applied successfully to Right Whales (Mate, Mesecar & Krutzikowsky, 1993) will provide information on ranges and migratory movements of individuals. Finally, it is to be hoped that focal animal studies (long neglected by investigators of mysticetes) will be undertaken to investigate the behaviour and association patterns of individual Humpbacks of different sex and age classes in both the high- and low-latitude ranges of this species.

ACKNOWLEDGMENTS

I thank Paul Racey, Phil Hammond and Ian Patterson for critical reviews of earlier drafts of this manuscript, and Tony Martin's thoughtful comments improved the final version. I also thank David Mattila and other colleagues at the Center for Coastal Studies for all their hard work in the study of Humpback Whales. Partial funding for the writing of this review through a postdoctoral fellowship from the American-Scandinavian Foundation is gratefully acknowledged.

LITERATURE CITED

- Alexander, R.D. 1975. Natural selection and specialized chorusing behaviour in acoustical insects. In: D. Pimental (ed.), *Insects, science and society*, pp. 35-77. New York: Academic Press.
- Amos, W., Schlötterer, C. & Tautz, D. 1993. Social structure of pilot whales revealed by analytical DNA profiling. *Science* 260: 670-672.
- Anderson, C.M. 1986. Female age: male preference and reproductive success in primates. *International Journal of Primatology* 7: 305-326.
- Armitage, K.B. 1987. Do female yellow-bellied marmots adjust the sex ratios of their offspring? *American Naturalist* 129: 501-519.
- Baker, C.S. & Herman, L.M. 1981. Migration and local movement of humpback whales (*Megaptera novaeangliae*) through Hawaiian waters. *Canadian Journal of Zoology* 59: 460-469.
- Baker, C.S. & Herman, L.M. 1984a. Seasonal contrasts in the behavior of the humpback whale. *Cetus* 5: 14-16.
- Baker, C.S. & Herman, L.M. 1984b. Aggressive behavior between humpback whales (*Megaptera novaeangliae*) wintering in Hawaiian waters. *Canadian Journal of Zoology* 62: 1922-1937.
- Baker, C.S., Herman, L.M., Perry, A., Lawton, W.S., Straley, J.M. & Straley, J.H. 1985. Population characteristics and migration of summer and late season humpback whales (*Megaptera novaeangliae*) in southeastern Alaska. *Marine Mammal Science* 1: 304-323.
- Baker, C.S., Palumbi, S.R., Lambertsen, R.H., Weinrich, M.T., Calambokidis, J. & O'Brien, S.J. 1990. Influence of seasonal migration on geographic distribution of mitochondrial DNA haplotypes in humpback whales. *Nature (London)* 344: 238-240.
- Baker, C.S., Perry, A., Bannister, J.L., Weinrich, M.T., Abernethy, R.B., Calambokidis, J., Lien, J., Lambertsen, R.H., Urbán Ramirez, J., Vásquez, O., Clapham, P.J., Alling, A., O'Brien, S.J. & Palumbi, S.R. 1993. Abundant mitochondrial DNA variation and world-wide population structure in humpback whales. *Proceedings of the National Academy of Science* 90: 8239-8243.
- Baker, C.S., Perry, A. & Herman, L.M. 1987. Reproductive histories of female humpback whales, *Megaptera novaeangliae*, in the North Pacific. *Marine Ecology Progress Series* 41: 103-14.
- Balcomb, K.C. & Nichols, G. 1982. Humpback whale censuses in the West Indies. *Reports of the International Whaling Commission* 32: 401-406.
- Baraff, L.S., Clapham, P.J., Mattila, D.K. & Bowman, R. 1991. Feeding behaviour of humpback whales in low-latitude waters. *Marine Mammal Science* 7: 49-54.
- Barnard, C.J. & Burk, T. 1979. Dominance hierarchies and the evolution of "individual recognition". *Journal of Theoretical Biology* 81: 65-72.
- Berger, J. 1989. Female reproductive potential and its apparent evaluation by male mammals. *Journal of Mammalogy* 70: 347-358.
- Berglund, A., Magnhagen, C., Bisazza, A., König, B. & Huntingford, F. 1993. Female-female competition over reproduction.

Behavioural Ecology 4: 184-187.

- Bertram, B.C.R. 1976. Kin selection in lions and in evolution. In: P.P.G. Bateson & R.A. Hinde (eds.) *Growing points in ethology*. Cambridge: Cambridge University Press.
- Bigg, M.A., Olesiuk, P.F., Ellis, G.M., Ford, J.K.B. & Balcomb, K.C. 1990. Social organization and genealogy of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. *Reports of the International Whaling Commission* (Special Issue 12): 383-405.
- Birkhead, T.R. 1979. Mateguarding in the magpie, *Pica pica*. *Animal Behaviour* 27: 866-874.
- Boesch, C. 1991. The effects of leopard predation on grouping patterns of forest chimpanzees. *Behaviour* 117: 220-242.
- Bradbury, J.W. 1977. Lek mating behaviour in the hammer-headed bat. *Zeitschrift für Tierpsychologie* 45: 225-255.
- Bradbury, J.W. 1981. The evolution of leks. In: R.D. Alexander & D. Tinkle (eds.) *Natural selection and social behavior: recent research and new theory*, pp. 138-169. New York: Chiron Press.
- Bradbury, J.W. & Gibson, R.M. 1983. Leks and mate choice. In: P.P.G. Bateson (ed.), *Mate choice*, pp. 109-138. Cambridge: Cambridge University Press.
- Bronson, F.H. 1985. Mammalian reproduction: an ecological perspective. *Biology of Reproduction* 32: 1-26.
- Brown, H.L. 1945. Evidence of winter breeding of *Peromyscus*. *Ecology* 26: 308-309.
- Brown, M. & Corkeron, P. 1995. Pod characteristics of migrating humpback whales (*Megaptera novaeangliae*) off the East Australian coast. *Behaviour* (in press).
- Brown, M.R., Corkeron, P.J., Hale, P.T., Schultz, K.W. & Bryden, M.M. 1995. Evidence for a sex-segregated migration in the humpback whale (*Megaptera novaeangliae*). *Proceedings of the Royal Society of London, B*, 259: 229-234.
- Brownell, R.L. & Ralls, K. 1986. Potential for sperm competition in baleen whales. *Reports of the International Whaling Commission* (Special Issue 8): 97-112.
- Chittleborough, R.G. 1958. The breeding cycle of the female humpback whale, *Megaptera nodosa* (Bonnaterre). *Australian Journal of Marine & Freshwater Research* 9: 1-18.
- Chittleborough, R.G. 1965. Dynamics of two populations of the humpback whale, *Megaptera novaeangliae* (Borowski). *Australian Journal of Marine & Freshwater Research* 16: 33-128.
- Chu, K.C. 1988. Dive times and ventilation patterns of singing humpback whales (*Megaptera novaeangliae*). *Canadian Journal of Zoology* 66: 1322-1327.
- Chu, K.C. & Harcourt, P. 1986. Behavioral correlations with aberrant patterns in humpback whale songs. *Behavioural Ecology & Sociobiology* 19: 309-312.
- Chu, K. & Nieukirk, S. 1988. Dorsal fin scars as indicators of sex, age and social status in humpback whales (*Megaptera novaeangliae*). *Canadian Journal of Zoology* 66: 416-420.
- Clapham, P.J. 1992. The attainment of sexual maturity in humpback whales. *Canadian Journal of Zoology* 70: 1470-1472.
- Clapham, P.J. 1993a. Social organization of humpback whales on a North Atlantic feeding ground. *Symposia of the Zoological Society of London* 66: 131-145.
- Clapham, P.J. 1993b. The social and reproductive biology of North Atlantic humpback whales, *Megaptera novaeangliae*. Ph.D. thesis, University of Aberdeen, Scotland.

- Clapham, P.J. 1994. Maturational changes in patterns of association among male and female humpback whales. *Journal of Zoology London* 234: 265-274.
- Clapham, P.J., Baraff, L.S., Carlson, C.A., Christian, M.A., Mattila, D.K., Mayo, C.A., Murphy, M.A. and Pittman, S. 1993. Seasonal occurrence and annual return of humpback whales in the southern Gulf of Maine. *Canadian Journal of Zoology* 71: 440-443.
- Clapham, P.J., Bérubé, M.C. & Mattila, D.K. 1995. Sex ratio of the Gulf of Maine humpback whale population. *Marine Mammal Science* 11: 227-231.
- Clapham, P.J. & Mattila, D.K. 1988. Observations of migratory transits of two humpback whales. *Marine Mammal Science* 4: 59-62.

- Clapham, P.J., Mattila, D.K. and Palsbøll, P.J. 1993. High-latitude-area composition of humpback whale competitive groups in Samana Bay: further evidence for panmixis in the North Atlantic population. *Canadian Journal of Zoology* 71: 1065-1066.
- Clapham, P.J. & Mayo, C.A. 1987. Reproduction and recruitment of individually identified humpback whales, *Megaptera novaeangliae*, observed in Massachusetts Bay, 1979-1985. *Canadian Journal of Zoology* 65: 2853-2863.
- Clapham, P.J. & Mayo, C.A. 1990. Reproduction of humpback whales, *Megaptera novaeangliae*, observed in the Gulf of Maine. *Reports of the International Whaling Commission*, Special Issue 12: 171-175.
- Clapham, P.J., Palsbøll, P.J., Mattila, D.K. and Vásquez, O. 1992. Composition and dynamics of humpback whale competitive groups in the West Indies. *Behaviour* 122: 182-194.
- Clutton-Brock, T.H. 1989. Mammalian mating systems. *Proceedings of the Royal Society of London B* 236: 339-372.
- Clutton-Brock, T.H. & Albon, S.D. 1979. The roaring of red deer and the evolution of honest advertisement. *Behaviour* 69: 145-170.
- Clutton-Brock, T.H., Albon, S.D. & Guinness, F.E. 1986. Great expectations: dominance, breeding success and offspring sex ratios in red deer. *Animal Behaviour* 34: 460-471.
- Clutton-Brock, T.H., Guinness, F.E. & Albon, S.D. 1982. *Red deer: the behaviour and ecology of two sexes*. Chicago: Chicago University Press.
- Clutton-Brock, T.H. & Harvey, P.H. 1977. Primate ecology and social organization. *Journal of Zoology London* 183: 1-39.
- Clutton-Brock, T.H. & Iason, G.R. 1986. Sex ratio variation in mammals. *Quarterly Review of Biology* 61: 339-374.
- Cox, C.R. & LeBoeuf, B.J. 1977. Female incitation of male competition: a mechanism in sexual selection. *American Naturalist* 111: 317-335.
- Darling, J.D. 1983. Mating behavior of "Hawaiian" humpback whales (*Megaptera novaeangliae*). In: *Proceedings of the Fifth Biennial Conference on the Biology of Marine Mammals*, p. 21 (abstract). Lawrence, Kansas: Society for Marine Mammalogy.

- Darling, J.D., Gibson, K.M. & Silber, G. 1983. Observations on the abundance and behavior of humpback whales (*Megaptera novaeangliae*) off West Maui, Hawaii, 1977-1979. In: R.S. Payne (ed.) *Behaviour and communication of whales*, pp. 201-222. AAAS Selected Symposium no. 76. Boulder, CO: Westview Press.
- Darling, J.D. & Mori, K. 1993. Recent observations of humpback whales (*Megaptera novaeangliae*) in Japanese waters off Ogasawara and Okinawa. *Canadian Journal of Zoology* 71: 325-333.
- Darwin, C.R. 1871. *The descent of man, and selection in relation to sex*. New York: Appleton.
- Davies, N.B. 1978. Ecological questions about territorial behaviour. In: J.R. Krebs & N.B. Davies (eds.), *Behavioural ecology: an evolutionary approach*, pp. 317-350. Oxford: Blackwell Scientific Publications.
- Davies, N.B. & Halliday, T.R. 1978. Deep croaks and fighting assessment in toads, *Bufo bufo*. *Nature (London)* 274: 683-685.
- Dawbin, W.H. 1966. The seasonal migratory cycle of humpback whales. In: K.S. Norris (ed.) *Whales, dolphins and porpoises*, pp. 145-170. Berkeley, CA: University of California Press.
- Dolphin, W.F. 1985. Food availability may measurably affect reproductive success in humpback whales. In: Proceedings of the Sixth Biennial Conference on the Biology of Marine Mammals, Vancouver BC (unpaginated abstract). Lawrence, KS: Society for Maine Mammalogy.
- Dolphin, W.F. 1987. Observations of humpback whale (*Megaptera novaeangliae*), killer whale (*Orcinus orca*) interactions in Alaska: comparisons with terrestrial predator-prey relationships. *Canadian Field Naturalist* 101: 70-75.
- Dunbar, R.I.M. 1981. Intraspecific variations in mating strategy. In: P. Klopfer & P. Bateson (eds.) *Perspectives in ethology*, vol. 5, pp. 385-341. New York: Plenum Press.
- D'Vincent, C.G., Nilson, R.M. & Hanna, R.E. 1985. Vocalization and coordinated feeding behavior of the humpback whale in southeastern Alaska. *Scientific Reports of the Whales Research Institute* 36: 41-47.
- Emlen, S.T. & Oring, L.W. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197: 215-223.
- Enquist, M. & Leimar, O. 1990. The evolution of fatal fighting. *Animal Behaviour* 39: 1-9.
- Fenchel, T. 1974. Intrinsic rate of natural increase and the relationship with body size. *Oecologia (Berlin)* 14: 317-326.
- Fisher, R.A. 1958. *The genetical theory of natural selection*. Second edition. New York: Dover Publications.
- Florez-Gonzalez, L., Capella, J. & Rosenbaum, H. 1994. Attack of killer whales (*Orcinus orca*) on humpback whales (*Megaptera novaeangliae*) on a South American Pacific breeding ground. *Marine Mammal Science* 10: 218-222.
- Frankel, A.S. 1994. *Acoustic and visual tracking reveals distribution, song variability and social roles of humpback whales in Hawaiian waters*. Unpublished Ph.D. thesis. Manoa, Hawaii: University of Hawaii.
- French, J.M., Moore, G.F., Perry, G.C. & Long, S.E. 1989. Behavioural predictors of oestrus in domestic cattle, *Bos taurus*. *Animal Behaviour* 38: 913-919.
- Gaskin, D.E. 1982. *The ecology of whales and dolphins*. London: Heinemann Press.
- Geraci, J.R., Anderson, D.M., Timperi, R.J., St. Aubin, D.J., Early, G.A., Prescott, J.H. & Mayo, C.A. 1989. Humpback whales (*Megaptera novaeangliae*) fatally poisoned by dinoflagellate toxins. *Canadian Journal of Fisheries & Aquatic Science* 46: 1895-1898.
- Glockner-Ferrari, D.A. & Ferrari, M.J. 1985. Individual identification, behavior, reproduction and distribution of humpback whales, *Megaptera novaeangliae*, in Hawaii. *National Technical Information Service Report No. MMC-83/06*,

Springfield, VA.

- Glockner-Ferrari, D.A. & Ferrari, M.J. 1990. Reproduction in the humpback whale (*Megaptera novaeangliae*) in Hawaiian waters, 1975-1988: the life history, reproductive rates and behaviour of known individuals identified through surface and underwater photography. *Reports of the International Whaling Commission* (Special Issue 12): 161-169.
- Gould, J.L. & Gould, C.G. 1989. *Sexual selection*. New York: Scientific American Library.
- Gosling, L.M. & Petrie, M. 1981. The economics of social organization. In: C.R. Townsend & P. Calow (eds.) *Physiological ecology*, pp. 315-345. Oxford: Blackwell Scientific Publications.
- Grafen, A. 1990. Do animals really recognize kin? *Animal Behaviour* 39: 42-54.
- Green, W.C.H. & Rothstein, A. 1991. Sex bias or equal opportunity? Patterns of maternal investment in bison. *Behavioural Ecology & Sociobiology* 29: 373-384.
- Greenwood, P.J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* 28: 1140-1162.
- Hafez, E.S.E. & Schein, M.W. 1962. The behaviour of cattle. In: *The behaviour of domestic animals*. London: Balliere, Tyndall and Cox.
- Hain, J.H.W., Carter, G.R., Kraus, S.D., Mayo, C.A. & Winn, H.E. 1982. Feeding behaviour of the humpback whale, *Megaptera novaeangliae*, in the western North Atlantic. *Fishery Bulletin* 80: 259-268.
- Hamilton, W.D. 1963. The evolution of altruistic behavior. *American Naturalist* 97: 32-34.
- Hamilton, W.D. 1964. The genetical evolution of social behaviour. I, II. *Journal of Theoretical Biology* 7: 1-52.
- Hammond, P.S., Mizroch, S.A. & Donovan, G.P. 1990. Individual recognition of cetaceans: use of photoidentification and other techniques to estimate population parameters. *Reports of the International Whaling Commission* (Special Issue 12). Cambridge. 440 pp.
- Harcourt, A.H., Harvey, P.H., Larson, S.G. & Short, R.V. 1981. Testis weight, body weight and breeding systems in primates. *Nature (London)* 293: 55-57.
- Herman, L.M. & Antinaja, R.C. 1977. Humpback whales in the Hawaiian breeding waters: population and pod characteristics. *Scientific Reports of the Whales Research Institute* 29: 59-85.
- Hughes, A.L. 1986. Kin coalitions and social dominance. *Journal of Theoretical Biology* 123: 55-66.
- Ingebrigtsen, A. 1929. Whales caught in the North Atlantic and other seas. *Reports of the Council for International Exploration of the Sea* 56: 1-26.
- James, W.H. 1986. Hormonal control of sex ratio. *Journal of Theoretical Biology* 118: 427-441.
- James, W.H. 1989. Parental hormone levels and mammalian sex ratios at birth. *Journal of Theoretical Biology* 139: 59-67.
- Johnson, C.N. 1986. Sex-biased philopatry and dispersal in mammals. *Oecologia (Berlin)* 69: 626-627.
- Katona, S.K. & Beard, J.A. 1990. Population size, migrations and feeding aggregations of the humpback whale (*Megaptera novaeangliae*) in the western North Atlantic Ocean. *Reports of the International Whaling Commission* (Special Issue 12): 295-305.
- Katona, S.K. & Whitehead, H.P. 1981. Identifying humpback whales using their natural markings. *Polar Record* 20: 439-444.
- Kent, J.P. 1992. Birth sex ratios in sheep over six lambing seasons. *Behavioural Ecology & Sociobiology* 30: 151-155.

- Kraus, S.D. 1986. A review of the status of right whales (*Eubalaena glacialis*) in the western North Atlantic with a summary of research and management. *National Technical Information Service*, report number PB86-154143. Springfield, Virginia.
- Krebs, J.R. & Davies, N.B. 1987. *An introduction to behavioural ecology*. Second edition. Oxford: Blackwell Scientific Publications.
- LeBoeuf, B.J. 1974. Male-male competition and reproductive success in elephant seals. *American Zoologist* 14: 163-176.
- Lee, R. 1970. Latitude and photoperiodism. *Archives of Meteorology, Geophysics & Bioclimatology Series B* 18: 325-332.
- Lenington, S. 1980. Female choice and polygyny in red-winged blackbirds. *Animal Behaviour* 28: 347-361.
- Leuthold, W. 1977. *African ungulates*. New York: Springer-Verlag.
- Lima, S.L. & Dill, L.M. 1990. Behavioral decisions made under the risk of predation. *Canadian Journal of Zoology* 68: 619-640.
- Lockyer, C.L. 1981. Growth and energy budgets of large baleen whales from the southern hemisphere. *Food and Agricultural Organization of the United Nations Fisheries Series* 5: 379-487.
- Lockyer, C.L. 1987. The relationship between body fat, food resource and reproductive energetic costs in North Atlantic fin whales (*Balaenoptera physalus*). *Symposia of the Zoological Society of London* 57: 343-361.
- Lott, D.F. 1984. Intraspecific variation in the social systems of wild vertebrates. *Behaviour* 88: 266-325.
- Marler, P. & Hamilton, W.J. 1966. *Mechanisms of animal behavior*. New York: Wiley & Sons.
- Mate, B.R., Mesecar, R. & Krutzikowsky, G. 1993. Satellite-monitored movements of bowhead whales. In: *Proceedings of the Tenth Biennial Conference on the Biology of Marine Mammals*, Galveston, TX (abstract). Lawrence, KS: Society for Marine Mammalogy.
- Matthews, L.H. 1937. The humpback whale, *Megaptera nodosa*. *Discovery Reports* 17: 7-92.
- Mattila, D.K. & Clapham, P.J. 1989. Humpback whales, *Megaptera novaeangliae*, and other cetaceans on Virgin Bank and in the northern Leeward Islands, 1985 and 1986. *Canadian Journal of Zoology* 67: 2201-2211.
- Mattila, D.K., Clapham, P.J., Katona, S.K. & Stone, G.S. 1989. Population composition of humpback whales, *Megaptera novaeangliae*, on Silver Bank, 1984. *Canadian Journal of Zoology* 67: 281-285.
- Mattila, D.K., Clapham, P.J., Vásquez, O. and Bowman, R. 1994. Occurrence, population composition and habitat use of humpback whales in Samana Bay, Dominican Republic. *Canadian Journal of Zoology* 72: 1898-1907.
- Mattila, D.K., Guinee, L.N. & Mayo, C.A. 1987. Humpback whale songs on a North Atlantic feeding ground. *Journal of Mammalogy* 68: 880-883.
- McHugh, T. 1958. Social behavior of the American buffalo (*Bison bison bison*). *Zoologica* 43: 1-40.
- McSweeney, D.J., Chu, K.C., Dolphin, W.F. & Guinee, L.N. 1989. North Pacific humpback whale songs: a comparison of southeast Alaskan feeding ground songs and Hawaiian wintering ground songs. *Marine Mammal Science* 5: 116-138.
- Medrano, L., Salinas, I., Salas, P., Ladrón de Guevara, P., Aguayo, A., Jacobsen, J. & Baker, C.S. 1994. Sex identification of humpback whales, *Megaptera novaeangliae*, on the wintering grounds of the Mexican Pacific Ocean. *Canadian Journal of Zoology* 72: 1771-1774.

- Mikhailiev, Y.A. 1995. Humpback whales of the Arabian Sea. *Reports of the International Whaling Commission* 47 (in press).
- Mobley, J.R. & Herman, L.M. 1985. Transience of social affiliations among humpback whales (*Megaptera novaeangliae*) on the Hawaiian wintering grounds. *Canadian Journal of Zoology* 63: 763-772.
- Mobley, J.R., Herman, L.M. & Frankel, A.S. 1988. Responses of wintering humpback whales (*Megaptera novaeangliae*) to playback of recordings of winter and summer vocalizations and of synthetic sound. *Behavioural Ecology & Sociobiology* 23: 211-223.
- Moss, C.J. 1983. Oestrous behaviour and female choice in the African elephant. *Behaviour* 86: 167-196.
- Mueller, U. 1993. Social status and sex. *Nature (London)* 363: 490.
- Nemoto, T. 1957. Foods of baleen whales in the northern Pacific. *Scientific Reports of the Whales Research Institute* 12: 33-89.
- Nishiwaki, M. 1959. Humpback whales in Ryukyuan waters. *Scientific Reports of the Whales Research Institute* 14: 49-87.
- Nishiwaki, M. 1966. Distribution and migration of the larger cetaceans in the North Pacific as shown by Japanese whaling results. In: Norris, K.S. (ed.) *Whales, dolphins and porpoises*. Berkeley, CA: University of California Press. Pp. 171-191.
- Ohno, M. & Fujino, K. 1952. Biological investigations on the whales caught by the Japanese Antarctic whaling fleets, season 1950/51. *Scientific Reports of the Whales Research Institute* 21: 1-78.
- Ohsumi, S. 1966. Allomorphis between body length at sexual maturity and body length at birth in the cetacea. *Journal of the Mammal Society of Japan* 3: 3-7.
- Omura, H. 1953. Biological study on humpback whales in the Antarctic whaling Areas IV and V. *Scientific Reports of the Whales Research Institute* 8: 81-102.
- Omura, H. Ohsumi, S., Nemoto, T., Nasu, K. & Kasuya, T. 1969. Black right whales in the North Pacific. *Scientific Reports of the Whales Research Institute* 21: 1-78.
- Overholtz, W.J. & Nicolas, J.R. 1979. Apparent feeding by the fin whale, *Balaenoptera physalus*, and the humpback whale, *Megaptera novaeangliae*, on the American sandlance, *Ammodytes americanus*, in the Northwest Atlantic. *Fishery Bulletin* 77: 285-287.
- Packer, C., Gilbert, D.A., Pusey, A.E. & O'Brien, S.J. 1991. A molecular genetic analysis of kinship and cooperation in African lions. *Nature (London)* 351: 562-565.
- Palsbøll, P.J., Clapham, P.J., Mattila, D.K., Larsen, F., Sears, R., Siegismund, H.R., Sigurjónsson, J., Vásquez, O. and Arctander, P. 1995. Distribution of mtDNA haplotypes in North Atlantic humpback whales: the influence of behavior on population structure. *Marine Ecology Progress Series* 116: 1-10.
- Parker, E.D. 1970. Sperm competition and its evolutionary consequences in the insects. *Biological Review* 45: 263-281.
- Parker, G.A. 1978. Evolution of competitive mate searching. *Annual Review of Entomology* 23: 290-303.
- Payne, P.M., Nicolas, J.R., O'Brien, L. & Powers, K.D. 1986. Distribution of the humpback whale, *Megaptera novaeangliae*, on Georges Bank and in the Gulf of Maine in relation to densities of the sand eel, *Ammodytes americanus*. *Fishery Bulletin* 84: 271-277.
- Payne, R.S. & Dorsey, E.M. 1983. Sexual dimorphism and aggressive use of callosities in right whales (*Eubalaena australis*). In: R.S. Payne (ed.) *Behaviour and communication of whales*, pp. 295-329. AAAS Selected Symposium no. 76.

Boulder, CO: Westview Press.

Payne, R.S. & McVay, S. 1971. Songs of Humpback Whales. *Science* 173: 585-597.

Payne, K., Tyack, P. & Payne, R. 1983. Progressive changes in the song of humpback whales (*Megaptera novaeangliae*): a detailed analysis of two seasons in Hawaii. In: R. Payne (ed.) *Communication and behavior of whales*, pp. 9-57. AAAS Symposia Series. Boulder, Colorado: Westview Press.

Pedersen, T. 1952. A note on humpback oil and on the milk and milkfat from this species (*Megaptera nodosa*). *Norsk Hvalfangsttidende* 41: 375-378.

Perry, A., Baker, C.S. & Herman, L.M. 1990. Population characteristics of individually identified humpback whales in the central and eastern North Pacific: a summary and critique. *Reports of the International Whaling Commission* (Special Issue 12): 307-317.

Poole, J.H. 1989. Mate guarding, reproductive success and female choice in African elephants. *Animal Behaviour* 37: 842-849.

Poole, J.H., Payne, K.A., Langubauer, W.R. & Moss, C.J. 1988. The social contexts of some very low frequency calls of African elephants. *Behavioural Ecology & Sociobiology* 22: 385-392.

Ralls, K. 1976. Mammals in which females are larger than males. *Quarterly Review of Biology* 51: 245-270.

Ralls, K. 1977. Sexual dimorphism in mammals: avian models and unanswered questions. *American Naturalist* 111: 917-938.

Reeves, R.R., Leatherwood, S. & Papastravrou, V. 1991. Possible stock affinities of humpback whales in the northern Indian Ocean. *UNEP Marine Mammal Technical Report* 3: 259-269.

Rubenstein, D.I. 1980. On the evolution of alternative mating strategies. In: J.E.R. Staddon (ed.) *Limits to action*, pp. 65-100. London: Academic Press.

Rubenstein, D.I. & Wrangham, R.W. 1986. Socioecology: origins and trends. In: D.I. Rubenstein & R.W. Wrangham (eds.), *Ecological aspects of social evolution*, pp. 3-20. Princeton, NJ: Princeton University Press.

Rutberg, A.T. 1986. Lactation and fetal sex ratios in American bison. *American Naturalist* 127: 89-94.

Sinclair, A.R.E. 1977. *The African buffalo: a study of resource limitation of populations*. Chicago: University of Chicago Press.

Skogland, T. 1986. Sex ratio variation in relation to maternal condition and parental investment in wild reindeer, *Rangifer t. tarandus*. *Canadian Journal of Zoology* 64: 416-419.

Slijper, E.J. 1962. *Whales*. Ithaca, NY: Cornell University Press. 511 pp.

Stone, G.S., Florez-Gonzalez, L. & Katona, S. 1990. Whale migration record. *Nature (London)* 346: 705.

Straley, J.M. 1990. Fall and winter occurrence of humpback whales (*Megaptera novaeangliae*) in southeastern Alaska. *Reports of the International Whaling Commission* (Special Issue 12): 319-323.

Swartz, S. 1986. Gray whale migratory, social and breeding behavior. *Reports of the International Whaling Commission* (Special Issue 8): 207-229.

Swingle, W.M., Barco, S.G., Pitchford, T.D., McLellan, W.A. & Pabst, D.A. 1993. Appearance of juvenile humpback whales feeding in the nearshore waters of Virginia. *Marine Mammal Science* 9: 309-315.

Symons, H.W. & Weston, R.D. 1958. Studies on the humpback whale (*Megaptera nodosa*) in the Bellinghausen Sea. *Norsk Hvalfangsttidende* 47: 53-81.

- Thomas, D.C., Barry, S.J. & Kiliaan, H.P. 1989. Fetal sex ratios in caribou: maternal age and condition effects. *Journal of Wildlife Management* 53: 885-890.
- Thomson, A.M. 1959. Maternal stature and reproductive efficiency. *Eugenics Review* 51: 157-162.
- Thornhill, R. & Alcock, J. 1983. *The evolution of insect mating systems*. Cambridge, Massachusetts: Harvard University Press.
- Thouless, C.R. & Guinness, F.E. 1986. Conflict between red deer hinds: the winner always wins. *Animal Behaviour* 34: 1166-1171.
- Trivers, R.L. & Willard, D.E. 1973. Natural selection of parental ability to vary the sex ratio of offspring. *Science* 179: 90-92.
- Tyack, P. 1981. Interactions between singing Hawaiian humpback whales and conspecifics nearby. *Behavioural Ecology & Sociobiology* 8: 105-116.
- Tyack, P. 1983. Differential responses of humpback whales, *Megaptera novaeangliae*, to playback of song or social sounds. *Behavioural Ecology & Sociobiology* 13: 49-55.
- Tyack, P. & Whitehead, H. 1982. Male competition in large groups of wintering humpback whales. *Behaviour* 83: 1-23.
- Verme, L.J. 1985. Progeny sex ratio relationships in deer: theoretical vs. observed. *Journal of Wildlife Management* 49: 134-136.
- Waldman, B. 1987. Mechanisms of kin recognition. *Journal of Theoretical Biology* 128: 159-185.
- Wasser, S.K. 1983. *Social behavior of female vertebrates*. New York: Academic Press.
- Watkins, W.A. & Schevill, W.E. 1979. Aerial observation of feeding behavior in four baleen whales. *Journal of Mammalogy* 60: 155-163.
- Weinrich, M.T. 1991. Stable social associations among humpback whales (*Megaptera novaeangliae*) in the southern Gulf of Maine. *Canadian Journal of Zoology* 69: 3012-3019.
- Weinrich, M.T., Bove, J. & Miller, N. 1993. Return and survival of humpback whale (*Megaptera novaeangliae*) calves born to a single female in three consecutive years. *Marine Mammal Science* 9: 325-328.
- Weinrich, M.T. & Kuhlberg, A.E. 1991. Short-term association patterns of humpback whales (*Megaptera novaeangliae*) groups on their southern Gulf of Maine feeding grounds. *Canadian Journal of Zoology* 69: 3005-3011.
- Weinrich, M.T., Schilling, M.R. & Belt, C.R. 1992. Evidence for acquisition of a novel feeding behaviour: lobsailing feeding in humpback whales, *Megaptera novaeangliae*. *Animal Behaviour* 44: 1059-1072.
- Western, D. 1979. Size, life history and ecology in mammals. *Afr. J. Ecol.* 17: 185-204.
- Whitehead, H.P. 1981. *The behaviour and ecology of Northwest Atlantic humpback whales*. Unpublished Ph.D. thesis. Cambridge: University of Cambridge.
- Whitehead, H. 1983. Structure and stability of humpback whale groups off Newfoundland. *Canadian Journal of Zoology* 61: 1391-1397.
- Whitehead, H.P. & Glass, C. 1985. Orcas (killer whales) attack humpback whales. *Journal of Mammalogy* 66: 183-185.
- Whitehead, H. & Moore, M.J. 1982. Distribution and movements of West Indian humpback whales in winter. *Canadian Journal of Zoology* 60: 2203-2211.
- Wiley, D.N. and Clapham, P.J. 1993. Does maternal condition affect the sex ratio of offspring in humpback whales? *Animal Behaviour* 46: 321-324.

- Wiley, R.H. 1978. Lek mating system of the sage grouse. *Scientific American* 238: 114-125.
- Wilson, E.O. 1975. *Sociobiology: the new synthesis*. Harvard: Belknap.
- Winn, H.E., Edel, R.K. & Taruski, A.G. 1975. Population estimate of the humpback whale (*Megaptera novaeangliae*) in the West Indies by visual and acoustic techniques. *Journal of the Fisheries Research Board of Canada* 32: 499-506.
- Winn, H.E. & Winn, L.K. 1978. The song of the humpback whale, *Megaptera novaeangliae*, in the West Indies. *Marine Biology* 47: 97-114.
- Wittenberger, J.F. 1979. Evolution of mating systems in birds and mammals. In: P. Marler & J.G. Vandenberg (eds.), *Handbook of behavioral neurobiology, vol. 3: Social behavior and communication*, pp. 271-349. New York: Plenum Press.
- Woolfenden, G.E. & Fitzpatrick, J.W. 1984. *The Florida scrub jay*. Princeton, NJ: Princeton University Press.