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The Nature of Humpback Whale (Megaptera novaeangliae) Song

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Abstract
The nature of humpback whale (*Megaptera novaeangliae*) song has long interested both scientists and the general public. Research strongly indicates that humpback whale song is an important component in the social behaviour of breeding humpback whales, with proposals that the song has an intra- and/or inter-sexual selection component. Some scientists, however, have alternate hypotheses, such as song being a means of sonar for detecting females. Song is not the only factor involved in humpback whale breeding behaviour, as groups of males follow and may physically compete for females. Hence, the exact nature of humpback whale song and its relation to their breeding behaviour is unclear. Why does whale song continuously change throughout the breeding season, and why do new songs spread so quickly throughout a population? In many respects, the nature of humpback whale song may resemble and parallel bird song. For example, many bird species that display innovation in the male's song also have increased reproductive fitness, and a similar situation may occur in male humpback whales. To explain why such innovation may be selected for in humpback whales, this paper postulates that sexual selection in humpback whales may have both a physical and cognitive fitness component.

"*No one knew why humpbacks sang. Nate had been listening to them, observing them, photographing them, and poking them with sticks for twenty-five years, and still he had no idea why, exactly, they sang*".
From Christopher Moore. *Fluke. Or I know why the winged whale sings*. Harper Collins. 2004.

Introduction

Why do male humpback whales (*Megaptera novaeangliae*) sing? The purpose and nature of the captivating songs of the humpbacks have been an enigma for modern zoologists ever since they were first discovered by scientists (79). Opinions as to the purpose of humpback song varies widely, from the calls being no different to those of herding animals to the idea that they may be a way of transmitting highly complex information, perhaps even being equivalent to language. There is debate as to whether the song is a mating call (vocalisation that contains information about the breeding intentions of the caller), a way of defending an area such as a territory (an area occupied and defended by one or more animals against conspecifics through overt defence or advertisement), a means of co-ordinating co-operation between males, a combination of these functions, or an as yet undetermined function. This theoretical paper seeks to review information on the nature of humpback song and the hypotheses as to its function, and to suggest some new hypotheses.

Humpback whale behaviour

Humpback whales (humpbacks) typically undertake extensive seasonal migration between high latitude summer feeding grounds and low latitude, tropical winter reproductive areas (*c.f.*, Arabian Sea population; 63). On the high latitude feeding grounds, several of them will associate and co-ordinate with each other to produce "bubble nets" that aid in trapping and herding shoaling fish (98). Humpbacks appear to have traditional feeding and breeding grounds as they return to particular local habitats and regional feeding areas, which seems to be a result of early experience and maternal influence. Craig and Herman (26) and Weinrich (101) documented these results through individual return rates and population genetics in the southern Gulf of Maine and on the breeding grounds off the Hawaiian Islands. Research also shows that individuals from various feeding grounds may use one breeding area, presumably to increase their mating opportunities, although humpbacks from one breeding area may also visit several feeding grounds (12,90).

Craig and Herman (26) suggested that not all females completed or even began the migration to Hawaii each year, as they may have become pregnant prior to migrating and returned to, or remained on, their feeding grounds. Some females along eastern Australia also remained in feeding grounds during winter (11). As a result, a biased sex ratio of 2.4 males to 1 female was found in both north- and southbound migrations off eastern Australia by Brown *et al.* (11). This consequently limits the number of females on the winter breeding grounds. As males outnumber females, males have to compete physically for proximity to females (27).

Furthermore, sexual segregation has been observed during the migration from the North Atlantic feeding grounds to the breeding grounds in the West Indies (90). Male humpbacks migrating off eastern Australia, associating together frequently, were found in larger groups than females (10). Males from all feeding grounds also arrive earlier at the breeding area in the West Indies than do females (90).

Finally, comparing females with and without calves during the progression of the breeding season, Craig *et al.* (27) found that males in Hawaii associate preferentially with, and competed more vigorously for, females without a calf (*i.e.*, females with high reproductive potential). This criterion appeared to be less important as the breeding season progressed, presumably as the number of births significantly reduced the availability of calf-less females. These various findings set the scene for very active male competition for breeding females.

Not all humpback populations migrate, however. Mikhalev (63) argued that there is at least one population in the Arabian Sea that remains in these subtropical-tropical waters year-round and noted that this was unusual for the species. As the Arabian Sea is the site of a major oceanic upwelling, productiv-

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ity in this area is high due to abundant nutrients, warm surface waters and abundant sunlight, and so humpbacks in this region may have no need to migrate long distances away from tropical waters to find sufficient food.

The organisation of whale groups on breeding grounds may be more complex than during feeding or migration. Spitz *et al.* (86) examined both the social role of males and group size in humpbacks on winter breeding areas of the Hawaiian Islands in relation to body length. They found that females were larger than males and were rarely found with other females, and also that the sex ratio on the breeding ground was two males to one female. Spitz *et al.* (86) categorised males as principal escort, secondary escort, lone escort with mother-calf pair, male partner and singer. Principal escorts were significantly larger on average than other males except singers. Singers in turn were significantly larger than male partners, but no significant differences in size were found in other pairwise comparisons between the groups. Principal escorts also tended to be the largest or second largest male in their individual competitive group, and their size indicated that they had reached sexual maturity. Interestingly, the other categories of males may not be mature except singers. Group structure may also be a function of other factors, such as time of day, with Hawaiian adults generally being alone in morning and gathered into pods (a group of cetaceans), increasing in size over the day (46). This structure is important, as the breeding grounds are where the majority of male humpbacks are found singing. Male singers off Maui, Hawaii, were joined on occasion by other individual males, where the pair either split up or formed a group (32). Singing also occurs before and after male-male interactions during the breeding season (32). However, singing appears to be a solitary activity and does not necessarily result in immediate physical contact with females or other males.

Evidence suggests that humpbacks have a promiscuous mating system. Individually identified females were resighted with different male associates during at least two breeding seasons off the Gulf of Maine (20). Clapham and Palsboll (20) also found that the offspring of individual females had multiple paternities. This was further reinforced recently by the paternity analyses of Cerchio *et al.* (15), which also indicated a promiscuous mating system. The system was found not to be egalitarian, as some male humpbacks had a slightly greater reproductive success than others. In the sample analysed, most males were not attributed any paternities over the 5-year study, with rates of one or two paternities close to expected values from a random mating system. However, two to three males were assigned three paternities, which was significantly greater than expected (15).

Given the uneven sex ratio on the breeding grounds, a promiscuous mating system would probably produce competition between males for access to females, so there would likely be intra-sexual selection based upon ability to monopolize and defend a female. This competition may be physical, as aggression can occur within groups of males, especially when males are apparently competing for access to a female with or without a calf (8,42,96). Such male aggression can draw blood (8,33) and may possibly, on very rare occasions, be severe enough to result in the death of a male humpback (72).

Competitive behaviour has also been observed away from the breeding grounds in both north- and southbound migrations, although most male-male interactions were not agonistic and some were even co-operative in nature (10). However, physical aggression may not be the only method of competition

Picture 1. Humpback whale breaching - reproduced with permission Allan Whaley/FUNDEMAR

used by male humpbacks, and song may be a key technique. Here we introduce humpback song and then discuss possible causes and effects of males singing.

Humpback whale song

The structure of humpback whale song

The sounds produced by humpbacks are low to mid frequency, usually 30 Hz to 8 kHz (23,75,85,93). Peak frequencies are generally around 315Hz and 630Hz (5), although high frequencies of up to 24kHz may sometimes be reached (4,6,7). Although the higher frequency components of their calls would be relatively short range, the low frequency components can travel considerable distances. As a result, humpbacks are able to communicate over tens or hundreds of kilometres and may not need to be in close physical proximity to remain in contact (1).

A humpback song can be broken down into a number of “themes” (75). In turn, each theme contains a number of repetitions of a phrase. Phrases may last for 20-40 seconds, while entire songs may be longer than 30 minutes. Themes are generally sung in a particular order (75) and the singing whale can take about 10 minutes to come back to the original theme. The structure of the song is complex and hierarchical, consisting of short and long segments with multiple layers of repetition or periodicities that may contain six units or even 400 units (91). The song conveys one bit of information per second, compared to humans with approximately ten bits per second (91).

Light does not travel far underwater, particularly at depth, whereas sound travels faster underwater than through air. This renders vision underwater less effective than hearing as a means of communicating. In broadcasting and receiving sound underwater, there may be strategies that improve this mode further. For example, there would be less interference from the deep scattering layer at certain times of day or night, or with less stratification related to the diurnal vertical migration of plankton. Males may use the sound propagation properties of the top layer of the water. For example, sending a song along a thermocline would allow a broadcast to cover a wider horizontal area. This suggestion is supported by the findings of Au *et al.* (7), whereby the higher frequencies in humpback song, which do not travel as far as lower frequencies, are projected horizontally.

There are also indications of a diurnal pattern in sound pressure levels of whale song, whereby levels were significantly

louder at night during the breeding season in Hawaii (5). Sound levels increased during sunset and only decreased at sunrise. It has been suggested that this pattern may reflect song being sexual advertisement as the main male mating strategy at night, while vision may be key to the formation of competitive groups during the day (5). There are several other alternative explanations. For example, many animals rely on sound for communication at night, and the humpbacks may simply be compensating for the increase in ambient noise. Another possibility is that the whales are taking advantage of, or compensating for diurnal changes in oceanographic features, as discussed by Au *et al.* (5).

Song in other whales

Many baleen whales spend a significant percentage of their time producing loud low-frequency sounds (57). Some examples of the frequency of sounds produced can be seen in Table 1.

Many of these sounds are less elaborate than humpback whale vocalisations, with less structure, and are not generally considered to be songs. Even so, fin whales (*Balaenoptera physalus*) produce series of pulsed sounds that are directly associated with the reproductive season and are thought to be produced by the males (100). The same sound sequences are never repeated exactly and are thought to stimulate vocalisation in other fin whales, while the approach of another whale induces a calling animal to cease (100). Fin whale use of these signals suggests a similar function to the songs of humpbacks (100).

Common Name	Scientific Name	Frequency of Sounds Produced
[1]Right	*Balaena glacialis*	Largely below 500 Hz
[2]Minke	*B. acutorostrata*	60 Hz to 6 kHz
[3]Blue	*B. musculus*	12 to 222 Hz
[4]Bowhead	*B. mysticetus*	Largely below 1000 Hz
[5]Fin	*B. physalus*	About 20 Hz

Table 1. Examples of sounds produced by baleen whales
[1]22; [2]60; [3]28,57,83,87,88,89,92; [4]29,30,60; [5]100

The one other whale known to sing is the bowhead. These songs are simpler than those of humpbacks, consisting of many repetitions of a small number of sounds in the same order (54). They are produced during the spring migration (54), on or near the winter breeding grounds and may change from year to year in a similar manner to those of humpbacks. This could be an example of convergence in evolution, or it may indicate that the song predates the speciation of either the bowhead or humpbacks, suggesting that the original reason for the song may be different from the development of its unique complexity in the humpback.

The changing structure of whale song

Another interesting aspect of humpback song is that it is constantly changing over time (75). All the males in a humpback population within a region sing essentially the same song (77,104), which may have segments that overlap with songs belonging to adjacent populations. Humpback song is generally produced on the breeding grounds (17) and rarely produced on feeding grounds. When the males resume their song at the beginning of a new breeding season, the song is the same as at the end of the previous breeding season (75). As the breeding season progresses the songs of each population change in structure (74,75,78). Innovations by individuals are copied and incorporated into their songs by other males in the breeding site, until these changes are apparently adopted by all males (74,75). At the end of the breeding season males tend to cease singing until the following mating season. It has been suggested that song transmission is cultural, as the changes arise spontaneously and are incorporated by others as they arise (39), but there may also be some components of whale song that change independently of cultural exchange (16).

Comparisons with bird and bat song

The use of sound as song is not unique to humpbacks (62). The most studied form of song in animals is bird song, which generally functions as either a means of territorial defence from other males or a method of mate attraction and female selection. For example, song playback experiments have been carried out to show territorial defence in several bird species (*e.g.*, *Pardus major*; 51). Whales and songbirds may have a similar means of communication through convergent evolution. Birdsong is usually exclusive to males, as is the case in humpbacks (33,41,102) and is typically sung during the breeding season, which again is analogous to humpbacks, with a link to seasonal hormonal levels in birds. Although humpback song is sporadically heard in the summer feeding grounds (56,59), it is much more frequent both approaching and in the winter breeding grounds (81,103,104).

We may also be witnessing a two-strategy situation, as appears to occur in the male greater white-lined bats (*Saccopteryx bilineata*) in Trinidad. Males sing songs, while females produce only short calls (36). Males use a particular screech song in what appears to be marking a territory and a longer, more tonal call when interacting with females. Males with more complex songs were found to have more females in their territories, and females were found to be capable of distinguishing male from female ultrasonic sounds.

Song as Sonar to Detect Females

Magnusson and Kasuya (55) developed a probability model for male whale mating strategies, where females grouped in a pod and were receptive only briefly during the breeding season. They suggested a searching strategy for individual males which would be advantageous when: 1) a female is receptive a high percentage of time; and/or 2) a male is expected to locate a high number of pods in a breeding season. They noted that there was limited data available to test the model, but they suggested that sperm whales should benefit from this search strategy. Could the song of a humpback be a component of a search strategy?

In support of the theory that song is a searching mechanism, Frazer and Mercado (40) presented a long-range sonar model for humpback song. The sonar model suggests how singing males might find females, even though females generally ignore or avoid singers (32). It also suggests why males hardly ever sing while in the company of females or while competing with other males for the position of primary escort. They conclude that many cetacean vocalizations must have both a communication and a sonar function.

Au *et al.* (3) questioned a number of the assumptions in this model, considering the noise-limited form of the sonar equation, current understanding of humpback behaviour, and the characteristics of humpback songs. They also argued that

evolution should favour a stable signal if sonar is important to mating success by echolocation, but that in reality songs are plastic and change at a variable rate within each season, changing completely within about 5 years (74,75). However, all songs have some stable elements, such as the inclusion of specific frequencies broadcast at certain times and syllables of specific lengths; perhaps these are used as a searching mechanism. Whale song may have originated as a sonar mechanism that evolved, modifying the structure to incorporate other functions. However, a singer has never been observed localizing females (3). Moreover, if whale song is a form of sonar, why do whales not use it to detect conspecifics at all times? For example, on the feeding grounds song is not used when locating other animals to help in herding prey species. There would also be a strong argument for females to sing if it were used as sonar. However, most if not all of the above arguments apply only if sonar is the primary function of the song, not an incidental benefit from a signal used mostly for another reason.

Song as a Sexual Signal

Honest signalling and reproductive fitness

Many sexually-related signals in nature, including calls by vocal vertebrate species, are attempts to reflect fitness honestly by conveying the abilities of the signaller to the receiver (24,37,44,45,106,107,108). This might be an announcement of size or a display of fitness by essentially demonstrating how much of the signalling cost the signaller can absorb. This then allows a female to choose the best male possible to father her offspring or allow males to assess their competition.

The costs of producing a signal, such as a song, can be measured in terms of time and energy; that is, the energetic cost of signal production and the missed opportunities for breathing and foraging. Song production carries a notable energetic cost, through increased metabolic rate and energy consumption, as has been reported in birds (99). Costs may also be measured in terms of increased exposure to predators or advertising the singer's presence to their prey. These latter costs are likely to be negligible for humpbacks, as they rarely feed on the breeding grounds, and adults are not generally subject to predation.

If humpback songs are indeed an honest communication of fitness, the elements likely to indicate their physical fitness would include frequency (potentially linked to the size of the singer) and duration. Humpback songs can last for more than two hours (97,105) and the production of such a loud sound for such long periods of time certainly would be costly and would imply the intrinsic fitness of a singing male. Another option is that the time between breaths might convey size to a female or a competitor (19).

A recent study on swimming rates in male humpbacks suggests that singing during migration has additional costs. Noad and Cato (68) discovered that singing humpbacks, migrating between the Antarctic and Australia, swam much more slowly than non-singing whales (2.5 kmph versus 4 kmph). The slow swim speed may be the result of singing being physically costly, such that the energetic costs of singing preclude fast movement. There may also be an indirect cost of singing, whereby swimming at a slow speed reduces the amount of time males can spend feeding as the result of a prolonged migration to the feeding grounds in the Antarctic. As the value of the song must lie in how well it accomplishes its purpose, thus this behaviour must carry some additional benefit. For example, it might increase the number of females (if they are the targets for the song) exposed to an individual's song (68).

While key information on physical fitness may be conveyed by singing, this does not explain why songs are complex and yet consistent within a population. This suggests that they convey additional information. For example, the ability to remember a complex song might be an indicator of memory capacity and mental fitness.

Potential Benefits of Song

As discussed earlier, males appear to be competing for females: 1) directly through physical aggression or indirectly through male behaviour resulting in ranking in a social hierarchy; 2) indirectly through displays to females; or 3) a combination of both. Consequently, a male may have a number of attributes to bring to this competition, which may be used sequentially or as needed. As discussed above, it is possible that these attributes include vocalisation through song, along with size, strength, and social abilities.

Songs for Females

When singing whales join females, male behaviour thought to be associated with sexual activity is usually observed (95), which suggests that song could function as a sexual attractant. Although somewhat unusual, females have also been observed joining singers (60), further supporting this idea. Perhaps the broadcast of the male's song in a favourable place is important, as in the lek scenario discussed below. For example, a male might position himself at a point in the water column where the long distance transmission of sound is optimal, such as using a thermocline to produce a waveguide. A female receiving the song might be able to determine distance using received frequencies and then judge the male's relative fitness by the power of his song. Chu (19) also argued that indication of physical fitness could be conveyed through song structure correlating with breath-holding ability. This could be tested further, as there are many other characteristics, such as swimming speed, size, age and blood testosterone levels, that could equally be considered as indicative of male fitness and could feasibly be compared to song structure.

Male-Male Competition

Darwin (35) pointed out that courtship displays may also be directed at other males competing for females. That is, fitter males warn less fit males of their presence and that competition with them would ultimately be futile. In the case of humpbacks, this latter function would benefit both the singer, who would not have to exert himself to discourage other males, as well as the less fit males, who could suffer physically in a conflict with a stronger male. Darling and Bérubé (32) suggested that song is indeed for male-male communication or display due to the frequent cessation of song when one male joins another. They also noted that an escort may sing with a female -calf pair, adding further support to this idea.

Fertile females are likely to be a limiting resource for adult male humpbacks. Males may therefore use their song to compete against each other directly in a number of ways. One option is that the song is involved in establishing or indicating a male's position in a dominance hierarchy, as has been suggested by Darling (31) and Darling and Bérubé (32). There is some support for this as males tend to avoid or, on fewer occasions, charge at or approach (the latter term has been suggested as a more appropriate term by Darling) the playback of whale song, the latter presumably in a bid to displace a male

perceived to be of lower status (66,94). The results of these playback experiments are suggestive of territorial songs. Although males do not appear to hold physical territories, they may have simply gone unnoticed, as the distances involved could be large if they are maintained acoustically. Alternatively, it is quite possible that they may move their 'territories' if, like several pinnipeds (*e.g.*, northern elephant seal, *Mirounga angustirostris*; 53), they monopolise females rather than control other resources, as female humpbacks would be moving around unlike although female pinnipeds on a rookery.

Male and Female Receivers

If humpback songs appear territorial, but also seem to function as a sexual attractant, the communal display (in this case, singing) suggests that male humpbacks are using an area of water as a lekking arena (65). Leks are aggregations of displaying males to which females are attracted for mating. Jiguet *et al.* (49) define parameters for a lek as: a) no male parental investment occurs beyond sperm; b) males aggregate at specific sites for display; c) the only resource females find on a lek is the male; and d) females can select a mate (although this last parameter is disputed; see discussion in 21). An interesting example of a lekking bird is the only parrot to use such a mating system, the kakapo (*Strigops habroptilus*) (25). In the breeding season, the male settles into a bowl-like depression that he has dug in the ground at a suitable site and then begins a deep, resonant boom sound. In a good location, the boom can be broadcast over 5km. However, to address the lack of rigid spatial structure in the humpbacks 'territories' (or perhaps 'maritories'), Clapham (21) proposed the term 'floating lek'.

In a floating lek, a humpback male would use song to define an area as his 'territory'. Other males that hear the song could approach and attempt to displace the singer holding the area. Females might avoid singers for this reason, expecting and circumventing male-male confrontations by judging male fitness from a distance and remaining in the area if he measures up. Smaller humpbacks would be less able to compete directly and would be more likely to adopt alternative mating strategies, such as attempting to sneak into the 'territory' of an inattentive or otherwise occupied dominant male to mate with a coercible female. Sneaky mating is a strategy used in a wide variety of vertebrates, including various pinnipeds (*e.g.*, northern elephant seal: 53), and this scenario would explain the sizes of males reported by Spitz *et al.* (86). Singers would be trying to establish or maintain 'territories', primary escorts would be engaged in guarding a mate from smaller challengers (21) and the pairing of smaller males could represent a cooperative effort to gain access to a defended female (see below). It would follow that singers would sing more at night, in an effort to deter sneaky males from using darkness to hide their activities, as observed by Au *et al*. (5). It would also explain why more groups are seen later in the day (46), as sneaky males might tend to encroach on a singer's area more when he sings less.

Interestingly, playback experiments have shown that males will approach the social sounds made within a competitive group, more often than they approach song (66,94), which may indicate the use of a tactic reported in northern elephant seals. Less dominant males will often challenge a more dominant male when they have just finished a long fight and are exhausted, increasing the chances that the challenge will be successful (53).

A strategy of sneaking is a relatively inexpensive use of time and energy. Also, by not displaying, the sneaky male does not draw attention to himself from competitors or predators, although adult humpbacks on breeding grounds experience minimal predation pressure. Regardless, it is possible that a singer may receive (incidentally?) some environmental information from echoes produced by a song, such as the presence of other whales, as postulated by Frazer and Mercado (40). As mature females are larger than males, it is also possible that a singer can distinguish between a female, a large male and a smaller male. If females tend to remain at a distance from a singer, a singer might cease singing in order to join a female accompanied by a bold escort that the singer detected, protect his area and take the opportunity to mate.

Male-male cooperation

The majority of singers are lone males and while females are likely to hear the singing, it is generally only males that appear to move towards singers (32). Similarly, a singer usually stops singing when joined by another male (94), suggesting that the singing has either succeeded or failed to achieve its goal. It is thus likely that the goal is either to keep other males away (as discussed above), or to bring specific males closer to form a pair/group. As mentioned above, co-operation between males might be necessary in some cases to control females or force them into mating. It would also be easier for co-operating males to separate a female from her calf to facilitate mating. In primates, infants have been shown to disrupt attempts at mating (43). Gore (43) noted that successful males enticed the female to a position out of sight of the infant to mate with a cooperative female. However, the mother-offspring bond in humpbacks appears to be very strong.

Darling *et al.* (34) also hypothesised that male cooperation in mating could account for the song and singing as collaborative behaviour. They noted that males joining singers appear to behave co-operatively when escorting females. As a result they suggest that song may provide information on male-male associations over time with the changing nature of songs (see below) documenting a changing history of associations. They note that this may help document reciprocity when males assist each other when mating. However, this is not consistent with the agonistic interactions that have been reported by others (8,94).

Moreover, Noad *et al*. (67) reported that a song sung by two immigrant male humpbacks (from the western coast of Australia) was quickly incorporated by all the male singers in the entire eastern Australian population, within the space of a year. If whale song provided information on associations between males at another breeding ground, the rapid incorporation of this information by whales in a different area seems incongruous. Information on whales encountered on their own breeding ground would be more important than a record of male-male interactions where males are unlikely to meet.

The evolution of a complex call might have originally indicated that the singer was capable of a high level of co-operation and/or cognitive ability. Similarly, those who could memorise and reproduce the complex call would have been indicating the same. Thus new songs rapidly learnt/copied might have demonstrated the fitness of the individual males. As the song became more intricate, those less able to co-operate might have been excluded. However, currently singers and primary escorts are generally some of the larger males (86), whereas such co-operative efforts would more likely be

necessary among smaller males.

Changes and Novelty

As mentioned above, humpback whales change their song over time, presumably at some cost. Innovative processes take time and attention, as does listening to the songs of others for changes that then need to be learned and mastered. Whether innovating or copying, there should be some value in the alteration to justify the efforts.

Novel song could be the result of immigration (67), mistakes in learning (48), faulty repetition (possibly akin to genetic drift through mutation), or invention. The last example means innovation is conscious and requires directed effort on the whale's part; in this case, copying (imitation) might be less difficult or costly.

Some songbirds have been shown to invent or improvise song components (50,52), and a similar situation could be occurring in humpbacks. Analogies to the continuous evolution of whale song can also be found in birds. For example, the passerine saddleback (*Philesturnus carunculatus*) lives in semi-isolated populations with males preferring to settle in non-natal areas. Each population has its own song dialect. The dialects overlap, with some song themes shared by adjacent populations (48).

Nottebohm and Selander (70) suggest that dialects in birds reduce the gene flow between populations, but cross-breeding does occur. In fact, males that move into a new territory typically copy the songs sung by their new neighbours. In return, the established males copy aspects of the newcomer's song. This phenomenon is termed 'song-matching'. Song matching is known to occur in several other species, with the songs of immigrant birds being copied by endemic males (58).

Mutual copying seems to be limited in humpbacks, however. The arrival of singers from another population to the east Australian breeding population did not lead to a hybrid song, but to the population-wide adoption of the unfamiliar tune (67). Thus the situation in whales appears to involve other factors not encountered in bird species.

There are a number of outstanding questions regarding song-matching in humpbacks: why does the song change; why do changes spread throughout the whole breeding population until all are once again singing the same song; how do songs change; and by what mechanism do the changes spread? It is possible that males in different populations behave differently. The Arabian Sea population is thought to be non-migratory (63). A comparison of behaviour between this population and one that migrates would be a valuable test of this hypothesis.

Payne (77) suggested that by matching an established male's song, a younger male might disguise his presence and take advantage of the protection afforded to an established male. Thus a male keeping abreast of changes in a song might: 1) create an opportunity for sneaky mating; and/or 2) keep up with the competition. It seems unlikely that a sneaky male would want to advertise his position to the local established male at all. However, it is possible that song-matching reduces the competitive edge that larger animals have over smaller ones. To explore this fully, we would need to know who changes a song and if changing a song confers an advantage.

Cerchio *et al.* (16) alluded to the possibility that males producing innovative song have a selective advantage with respect to female mate choice. However, they did not offer a mechanism by which females would gain an adaptive advantage through mating with a male with an innovative song. Innovative song would have to be tied to a heritable trait that conferred survival or reproductive advantage for it to be a driving force behind mate selection. This would be the case if females assess male fitness through song in a way that is not reliant upon physical abilities, but through cognitive awareness. Alternatively, it is entirely possible that female mate choice based on song is self-supporting. That is, male offspring that display a particular trait are more likely to have numerous offspring of their own because females have a preference for it. This is known as Fisherian self-reinforcing selection (2).

If females are indeed assessing mental fitness they may prefer males who have newer songs, and perhaps the ability to innovate, or adopt innovations, is a trait that has value. Innovative song, or quick adoption of innovative song, may be an honest indicator of the ability for rapid cognitive response or initiation. However, the complex structure of the song and an ability to remember the constantly changing structure might also be an honest indicator of humpback memory. Memory must be an important contributor to a male's fitness, considering the long migratory routes of humpbacks. A recent study has observed unusual cortical architecture in humpbacks (compared to that of a fin whale, *Balaenoptera physalus*, and several odontocetes), which has previously been found only in hominids and the great apes, and is thought to be involved in processing complex behaviours (47).

Any female preference for males with a slightly different song structure may be selecting for a mate from outside the local population. For example, female European warblers (*Acrocephalus* spp.) prefer males who have more elaborate and unusual song structures (13,14). This could also be the case in humpbacks, with females being more receptive to males signalling elaborations of the normal song structure. Humpbacks have a relatively low reproductive rate and may be somewhat isolated, which could lead to inbreeding depression (18). Outsiders would have a substantially different genotype from the local males and inbreeding depression could be avoided if a female were to choose a mate with an unusual song to father her offspring. However, humpbacks found around the Pacific Ocean (Mexico, Hawaii and Japan) all share a similar song type, despite distinct genetic differences between whales from the various breeding populations (9). Furthermore, such selection would be complicated by innovation within a population.

It is also important to note that 'different' and 'novel' are not necessarily the same. The scenario above suggests that females value difference and not necessarily novelty. In that situation, some males would be expected to keep the original song or develop their own, as either would differ from the current song. However, it is possible that the true value of the songs does not lie in the fact that they are merely different. Consequently, novel song could be an important criterion in sexual selection. For example, in village indigo birds (*Vidua chalybeata*), males that spontaneously change songs, and are then imitated by other males, are more reproductively successful (76,77).

Mechanisms for change in song

The mechanism for change in humpback songs is unknown. As mentioned earlier, change in song could be a result of conscious effort or a random process. If it is a random process, the song could be considered a cultural version of a gene, known as a meme (38). Memes evolve more quickly than

genes, which could allow songs to become almost unrecognisable within 5-10 years (74,75), even though humpback songs change only during breeding seasons.

Any innovation, from whatever source, that provides additional advantage would spread quickly through a population with the ability to imitate. Each innovation represents a mutation in the structure of the meme, which then spreads through the population like a successful gene, but at a much faster rate. Genetic mutation is limited and will only modify the phenotypes that were present, with large changes taking many mutations. If meme mutation functions in the same way, only small changes would be possible, but these would be additive and become large differences quite quickly. Quicker change still would be expected if new memetic 'alleles' (*i.e.*, song elements) were introduced into the population.

This might have occurred when the vagrant whales first turned up in eastern Australia (67). If the memetic evolution in western Australia had taken a different path, conveying greater benefits, then the eastern whales with their ability to imitate may have recognised these benefits and switched memes. The more successful meme then spread throughout the population at the expense of the original one. This might explain why the western Australian whales did not simply begin singing the local song to fit in. Had they done this, it would mean that the value of a song is not in its novelty, but more likely within its elements or complexity. However, the fact that the eastern Australian whales adopted the song of the immigrants does not confirm selection for novelty or difference, as they may also have simply adopted an inherently better song for achieving whatever purpose it is for.

Random memetic mutations could arise from errors on the part of a whale resulting in the irreversibility and constantly changing structure of humpback song. One possible source of error could be rapid decay, reformation and rearrangement of memory-associated neurones in the brains of humpbacks. This is the case in canaries (*Serinus canaria*), which have a limited memory capacity and a need to constantly relearn mating song structure with a new song, replacing the old one in the memory neurones (69). With a song being constantly replaced, it would be inevitable that some learning errors would occur, leading to a change in song structure. However, there is little change in the form of humpback songs between the end of one breeding season and the beginning of the next, implying that the whales do not have a limited memory capacity.

These memetic changes could also be the result of a more active process, such as through active trial and error, with the members of the population (including the innovating whale) consciously or subconsciously assessing the worth of the variant and either adopting it, or abandoning it accordingly. An intriguing alternative to trial-and-error is intelligent innovation, with a whale pre-determining what could be a good adaptation to the song in terms of effective broadcast or female preference.

One other interesting possibility arises from the tendency of an animal to acclimate to signals to which it is repeatedly exposed. Acclimation to a signal potentially associated with a stressor involves a reduction of the physiological response to that signal, which often leads to increased physiological responses to novel signals (see 84). A similar heightened response would confer an advantage to whales seeking responses to their songs. Even if a physiological response isn't involved, it is likely that a new song would still be noticed more readily, as the possibility remains for females to 'tune out' signals (songs) to which they are repeatedly exposed.

Environmental Conditions and Song

Another option is that humpback males change their song in response to environmental conditions. Several species of animals change signals and displays to compensate for background noise in the environment. For example, two species of lizard (*Anolis cristatellus* and *A. gundlachi*) increase the speed of body movements used in visually 'noisy' environments (71). Short-term environmental variation is known to be a factor in temporary changes in humpback song. For example, humpbacks have modified their songs during exposure to low frequency sonar transmissions (64). Thus it is possible that song changes are the result of other short-term events, and leaves open the possibility that variability in environmental conditions throughout a season may lead to concurrent changes in songs.

Perhaps humpbacks arrive at the breeding ground and test the previous year's song in the current oceanographic conditions. In response to changing environmental factors, such as ambient sounds, eddies, temperature or salinity differences, or volcanic activity, the male humpbacks may modify their song in some way to improve detectability by increasing the signal-to-noise ratio, repeating certain features, or changing the frequencies involved. Many environmental features can persist over weeks or even months and thus the costs of modifying their song could be offset by the benefits to the males in broadcasting song.

Arms Races, Fashion and Relics

As discussed above, it could be that males in a population try to copy novel or better songs as quickly as possible to avoid being out-competed. This would result in a vocal arms race to produce a population-wide song structure that rapidly evolves throughout the breeding season. If this were the case, it would also be expected that when a male singing a novel or in some way better song enters a population (through immigration or innovation), other males would immediately start imitating this song to offset whatever advantage it conveys, as was reported by Noad *et al.* (67). Perhaps then the male song is equivalent to a vocal form of clothing; with most whales following the current trends in fashion, rather than expending energy resources on novelty.

It should be noted that it is also possible that the original driving force behind changing songs, as well as the reason that the males sing in the first place, may be an evolutionary relic. For example, if selection pressure was great enough, it may be that all whales that could not produce a complex song, or keep up with changes in that song, were unable to breed and are thus no longer represented within the population. This would mean that all males currently in the population now meet these original selection criteria. Despite the fact the physiological and behavioural mechanisms producing change could remain in place regardless, female choice or male competition must now involve more subtle differences between the songs, such as precise peak frequencies related to the size of the whale. For instance, the key of C played on a guitar and a banjo would have the same pitch but different overtones, which are subsidiary frequencies acting together. The result is differences in the quality of sound. It may also be that in their studies, researchers are missing such subtle differences between songs, possibly through the type of frequency filters that they use in their measurements.

Other hypotheses

Cetaceans are thought to have high cognitive awareness and culture (73,82) that might lead to the argument that singing is for pleasure, either of the male himself or for the female. Songs may still be a part of the male's mating strategy, but if it is pleasurable as well, this might increase the rate at which novel elements are produced or lead to the males singing more often. Song might also be carrying news that is updated by all singing males in increments, or even a collective current oral history. Information of this kind in the song might be valuable for survival (34). Alternatively, the primary function of the choral singing could be to synchronise oestrus in females (8).

Summary

There are numerous hypotheses concerning the nature of humpback song, many of which are not mutually exclusive. The logistical difficulties of studying the behaviour of humpbacks in comparison to songbirds render it challenging, although not impossible. In the meantime, it is a nice thought that, perhaps, humpback whales really are attracted to their mates for their minds.

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References

1. **Abileah R, Martin D, Lewis SD.** Long-range detection and tracking of humpback whale Hawaii-Alaska migration. *IEEE Oceans* 96:373-377. 1996.
2. **Andersson, MB.** *Sexual Selection*. Princeton, New Jersey: Princeton University Press, 1994.
3. **Au WWL, Frankel A, Helweg DA, Cato DH.** Against the humpback whale sonar hypothesis. *IEEE Journal of Oceanic Engineering* 26:295-300. 2001.
4. **Au WWL, James D, Andrews K.** High-frequency harmonics and source level of humpback whale songs. *Journal of the Acoustical Society of America* 110:2770. 2001.
5. **Au WWL, Mobley J, Burgess WC, Lammers MO, Nachtigall PE.** Seasonal and diurnal trends of chorusing humpback whales wintering in waters off western Maui. *Marine Mammal Science* 16:530-544. 2000.
6. **Au WWL, Pack, AA, Lammers MO, Herman L, Andrews K, Deakos M.** The acoustic field of singing humpback whales in the vertical plane. *Journal of the Acoustical Society of America* 113:2277. 2003.
7. **Au WWL, Pack, AA, Lammers MO, Herman L, Deakos M, Andrews K.** The acoustic properties of humpback whale songs. *Journal of the Acoustical Society of America* 120:1103-1110. 2006.
8. **Baker CS, Herman LM.** Aggressive behaviour between humpback whales (*Megaptera novaeangliae*) wintering in Hawaiian waters. *Canadian Journal of Zoology* 62:1922-1937. 1984.
9. **Baker CS, Medrano-González L, Calambokidis J, Perry A, Pichler FB, Rosenbaum H, Straley JM, Urban-Ramirez J, Yamaguchi M, Von Ziegesar O.** Population structure of nuclear intron and mitochondrial DNA variation among humpback whales in the North Pacific. *Molecular Ecology* 7:695-707. 1998.
10. **Brown M, Corkeron P.** Pod characteristics of migrating humpback whales (*Megaptera novaeangliae*) off the East Australian Coast. *Behaviour* 132:163-179. 1995.
11. **Brown MR, Corkeron PJ, Hale PT, Schultz KW, Bryden MM.** Evidence for a sex-segregated migration in the humpback whale (*Megaptera novaeangliae*). *Proceedings of the Royal Society of London, Series B* 259:229-234. 1995.
12. **Calambokidis J, Steiger GH, Straley JM, Herman LM, Cerchio S, Salden DR, Urbín RJ, Jacobsen J, vonZiegesar O, Balcomb KC, Gabriele CM, Dalheim ME, Uchida S, Ellisa G, Miyamura Y, Ladrón de Guevara P, Yamaguchi M, Sato F, Mizroch, SA, Schendler L, Rasmussen K, Barlow J, Quinn TJI.** Movements and population structure of humpback whales in the North pacific. *Marine Mammal Science* 17:769-794. 2001.
13. **Catchpole CK.** Sexual selection and the evolution of complex songs among European warblers of the genus *Acrocephalus*. *Behaviour* 74:149-166. 1980.
14. **Catchpole CK, Dittami J. Leisler B.** Differential responses to male song repertoires in female songbirds implanted with oestradiol. *Nature* 312:563-564. 1984.
15. **Cerchio S, Jacobsen JK, Cholewiak DM, Falcone EA, Merriwether DA.** Paternity in humpback whales, *Megaptera novaeangliae*: assessing polygyny and skew in male reproductive success. *Animal Behaviour* 70:267-277. 2005.
16. **Cerchio S, Jacobsen JK, Norris TF.** Temporal and geographical variation in songs of humpback whales, *Megaptera novaeangliae*: synchronous change in Hawaiian and Mexican breeding assemblages. *Animal Behaviour* 62:313-329. 2001.
17. **Charif RA, Clapham PJ, Clark CW.** Acoustic detections of singing humpback whales in deep waters off the British Isles. *Marine Mammal Science* 17:751-768. 2001.
18. **Charlesworth D, Charlesworth B.** Inbreeding depression and its evolutionary consequences. *Annual Review of Ecology and Systematics* 18:237-268. 1987.
19. **Chu K.** Dive times and ventilation patterns of singing humpback whales (*Megaptera novaeangliae*). *Canadian Journal of Zoology* 66:1322-1327. 1988.
20. **Clapham PJ, Palsboll PJ.** Molecular analysis of paternity shows promiscuous mating in female humpback whales (*Megaptera novaengliae*, Borowski). *Proceedings of the Royal Society of London, Series B* 264:95-98. 1997.
21. **Clapham PJ.** The social and reproductive biology of humpback whales: an ecological perspective. *Mammal Review* 26:27-49. 1996.
22. **Clark CW.** The acoustic repertoire of the southern right whale, a quantitative analysis. *Animal Behaviour* 30:1060-1071. 1982.
23. **Clark CW.** The acoustic behavior of mysticete whales. In: *Sensory Abilities of Cetaceans: Laboratory and Field Evidence*, edited by Thomas JA, Kastelein RA: Plenum Press, 1990.
24. **Clutton-Brock TH, Albon SD.** The roaring of red deer and the evolution of honest advertisement. *Behaviour* 69:145-170. 1979.
25. **Cockram JF, Rounce JR.** Non-invasive assessment of the annual gonadal cycle in free-living kakapo (Strigops habroptilus) using fecal steroid measurement. *The Auk* 112:253-257. 1995.
26. **Craig AS, Herman LM.** Sex differences in site fidelity and migration of humpback whales (*Megaptera novaeangliae*) to the Hawaiian Islands. *Canadian Journal of Zoology* 75:1923-1933. 1997.
27. **Craig AS, Herman LM, Pack AA.** Male mate choice and male-male competition coexist in the humpback whale (*Megaptera novaeangliae*). *Canadian Journal of Zoology* 80:745-755. 2002.
28. **Cummings WC, Thompson PO.** Underwater sounds from the blue whale, *Balaenoptera musculus*. *Journal of the Acoustical Society of America* 50:1193-8. 1971.
29. **Cummings CW, Holliday DV.** Sounds and source levels from bowhead whales off Pt. Barrow, Alaska. *Journal of the Acoustical Society of America* 82:814-821. 1987.
30. **Darling J.** Song. In: *Encyclopedia of Marine Mammals*, edited by Perrin WF, Würsig B, Thewissen JGM: Academic Press, 2002.
31. **Darling JD.** *Migrations, abundance and behaviour of 'Haiwaiian' humpback whales* (Megaptera novaeangliae). PhD thesis, University of California, Santa Cruz, 1983.
32. **Darling JD, Bérubé M.** Interactions of singing humpback whales with other males. *Marine Mammal Science* 17:570-584. 2001.
33. **Darling JD, Gibson KM, Silber GK.** Observations on the abun-

dance and behaviour of humpback whales (*Megaptera novaeangliae*) of West Maui, Hawaii, 1977-79. In: *Communication and Behaviour of Whales*, edited by Payne R: Westview Press, 1983.
34. **Darling JD, Jones ME, Nicklin CP.** Humpback whale songs: do they organize males during the breeding season? *Behaviour* 143:1051-1101. 2006.
35. **Darwin C.** *The Descent of Man and Selection in Relation to Sex*. London: Murray, 1971.
36. **Davidson SM, Wilkinson GS.** Function of male song in the greater white-lined bat, *Saccopteryx bilineata*. *Animal Behaviour* 67:883-891. 2004.
37. **Davies NB, Haliday TR.** Deep croaks and fighting assessment in toads *Bufo bufo*. *Nature* 274:683-685. 1978.
38. **Dawkins R.** *The Selfish Gene*. Oxford: Oxford University Press, 1976.
39. **Erikson N, Miller LA, Tougaard J, Helweg DA.** Cultural change in the songs of humpback whales (*Megaptera novaeangliae*) from Tonga. *Behaviour* 142:305-328. 2005.
40. **Frazer LN, Mercado E.** A sonar model for humpback whale song. *IEEE Journal of Oceanic Engineering* 25:160-182. 2000.
41. **Glockner DA.** Determining the sex of humpback whale (*Megaptera novaeangliae*) in their natural environment. In: *Communication and Behaviour of Whales*, edited by Payne R: Westview Press, 1983.
42. **Glockner-Ferrari DA, Ferrari MJ.** *Individual identification, behavior, reproduction, and distribution of humpback whales,* Megaptera novaeangliae, *in Hawaii.* The Marine Mammal Commission, Washington D.C., 1985.
43. **Gore, MA.** Mother-offspring conflict and interference at mother's mating in *Macaca fascicularis*, *Primates* 27:205-214. 1986
44. **Grafen A.** Biological signals as handicaps. *Journal of Theoretical Biology* 144:517-546. 1990a.
45. **Grafen A.** Sexual selection unhandicapped by the Fisher process. *Journal of Theoretical Biology* 144:473-516. 1990b.
46. **Helweg DA, Herman LM.** Diurnal patterns of behaviour and group membership of humpback whales (*Megaptera novaeangliae*) wintering in Hawaiian waters. *Ethology* 98:298-311. 1994.
47. **Hof PR, Van der Gucht E.** The structure of the cerebral cortex of the humpback whale, *Megaptera novaeangliae* (Cetacea, Mysticeti, Balaenopteridae). *Anatomical Record* 290:1-31. 2007.
48. **Jenkins HM.** Cultural transmission of birdsong. *Animal Behaviour* 26:74-77. 1978.
49. **Jiguet F, Arroyo B, Bretagnolle V.** Lek mating systems: a case study in the Little Bustard *Tetrax tetrax*. *Behavioural Processes* 51:63-82. 2000.
50. **Johnson, SL.** Do American robins acquire songs by both imitating and inventing? *Wilson Journal of Ornithology* 118:341-352. 2006.
51. **Krebs JR.** Territory and breeding density in the great tit *Parus major* L. *Ecology* 52:2-22. 1971.
52. **Kroodsma DE, Liu, W-C, Goodwin E, Bedell PA.** The ecology of song improvisation as illustrated by North American sedge wrens. *Auk* 116:373-386. 1999.
53. **Le Boeuf BJ.** Male-male competition and reproductive success in elephant seals. *American Zoologist* 14:163-176. 1974.
54. **Ljungblad DK, Thompson PO, Moore SE.** Underwater sounds recorded from migrating bowhead whales, *Balaena mysticetus*, in 1979. *Journal of the Acoustical Society of America* 71:477-482. 1982.
55. **Magnusson KG, Kasuya T.** Mating strategies in whale populations: searching strategy vs. harem strategy. *Ecological Modelling* 102:225-242. 1997.
56. **Mattila DK, Guinee LN, Mayo CA.** Humpback whale songs on a North Atlantic feeding ground. *Journal of Mammalogy* 68:880-883. 1987.
57. **McDonald MA, Hildebrand JA, Webb SC.** Blue and fin whales observed on a seafloor array in the Northeast Pacific. *Journal of the Acoustical Society of America*. 98:712-721. 1995.
58. **McGregor PK, Krebs JR.** Mating and song types in the great tit. *Nature* 297:60-61. 1982.
59. **McSweeny DJ, Chu KC, Dolphin WF, Guinee LN.** North Pacific humpback whale songs: a comparison of southeast Alaskan feeding ground songs and Hawaiian wintering ground songs. *Marine Mammal Science* 5:116-138. 1989.
60. **Medrano L, Salinas I, Salas P, Ladrón de Guevara P, Aguayo A, Jacobsen J, Baker CS.** Sex identification of humpback whales, *Megaptera novaeangliae*, on the wintering grounds of the Mexican Pacific Ocean. *Canadian Journal of Zoology* 72:1771-1774. 1994.
61. **Mellinger DK, Carson CD, Clark CW.** Characteristics of minke whale (*Balaenoptera acutorostrata*) pulse trains recorded near Puerto Rico. *Marine Mammal Science* 16:739–756. 2000.
62. **Mercado E III, Frazer LN.** Humpback whale song or humpback whale sonar? A reply to Au et al. *IEEE Journal of Oceanic Engineering* 26:406-415. 2001.
63. **Mikhalev YA.** Humpback whales *Megaptera novaeangliae* in the Arabian Sea. *Marine Ecology Progress Series* 149:13-21. 1997.
64. **Miller PJO, Biassoni N, Samuels A, Tyack PL.** Whale songs lengthen in response to sonar. *Nature* 405: 903. 2000.
65. **Mobley JR, Herman LM.** Transience of social affiliations among humpback whales (*Megaptera novaeangliae)* on the Hawaiian wintering grounds. *Canadian Journal of Zoology* 63:763-772. 1985.
66. **Mobley JR, Herman LM, Frankel AS.** Responses of wintering humpback whales (*Megaptera novaeangliae*) to playback recordings of winter and summer vocalisations and of synthetic sound. *Behavioral Ecology and Sociobiology* 23:211-223. 1988.
67. **Noad MJ, Cato DH, Bryden MM, Jenner M-N, Jenner KCS.** Cultural revolution in whale songs. *Nature* 408:537. 2000.
68. **Noad MJ, Cato DH.** Swimming speeds of singing and non-singing humpback whales during migration. *Marine Mammal Science* 23:481-495. 2007.
69. **Nottebohm F**. From bird song to neurogenesis. *Scientific American* 260:74-79. 1989.
70. **Nottebohm F, Selander RK.** Vocal dialects and gene flow frequencies in the Chingolo sparrow (*Zonotrichia capensis*). *Condor* 74:137-143. 1972.
71. **Ord TJ, Peters RA, Clucas B, Stamps JA.** Lizards speed up visual displays in noisy motion habitats. *Proceedings of the Royal Society of London, Series B* 274:1057-1062. 2007.
72. **Pack AA, Salden DR, Ferrari MJ, Glockner-Ferrari DA, Herman LM, Stubbs, HA, Straley JM.** Male humpback whale dies in competitive group. *Marine Mammal Science* 14:861-873. 1998.
73. **Parsons ECM, Rose NA, Simmonds M.** Whales – individuals, societies and cultures. In: *Troubled Waters*, edited by Brakes P, Butterworth A, Simmonds M, Lymbery, P: WSPA, 2004.
74. **Payne K, Payne R.** Large scale changes over 17 years in songs of humpback whales in Bermuda. *Zeitschrift für Tierpsychologie* 68:89-114. 1985.
75. **Payne K, Tyack P, Payne R.** Progressive changes in the song of humpback whales (*Megaptera novaeangliae*): a detailed analysis of two seasons in Hawaii. In: *Communication and Behaviour of Whales*, edited by Payne R: Westview Press, 1983.
76. **Payne RB.** Behavioral continuity and change in local song populations of village indigobirds (*Vidua chalybeate*). *Zeitschrift für Tierpsychologie* 70:1-44. 1985.
77. **Payne RB.** Microgeographic variations in songs of splendid sunbirds *Nectarinia coccinigaster*: Population phenetics, habitats, and song dialects. *Behavior* 65:282-308. 1978.
78. **Payne RS.** Behavior and vocalizations of humpback whales (*Megaptera* sp.). In: *Report on a Workshop on Problems Related to Humpback Whales (*Megaptera novaeangliae*) in Hawaii*, edited by Norris KS, Reeves RR: U.S. Department of Commerce, 1978.
79. **Payne RS, McVay S.** Songs of humpback whales. *Science* 179:585-597. 1971.
80. **Pearce JM.** *Animal Learning and Cognition*: Hove, U.K.: Psychology Press, 1997.
81. **Perkins J, Whitehead H.** Observations of three species of baleen whales off Newfoundland and adjacent waters. *Journal of the Fisheries Research Board of Canada* 34:1436-1440. 1977.

82. **Rendell L, Whitehead H.** Culture in whales and dolphins. *Behavioral and Brain Sciences* 24:309-382. 2001.
83. **Rivers JA.** Blue whale, *Balaenoptera musculus*, vocalizations from the waters off central California. *Marine Mammal Science 13*:186-195. 1997.
84. **Romero LM.** Physiological stress in ecology: Lessons from biomedical research. *Trends in Ecology and Evolution* 19:249-255. 2004.
85. **Silber GK.** The relationships of social vocalizations to surface behavior and aggression in the Hawaiian humpback whale (*Megaptera novaeangliae*). *Canadian Journal of Zoology* 64:2075-2080. 1986.
86. **Spitz SS, Herman LM, Pack AA, Deakos MH.** The relation of body size of male humpback whales to their social roles on the Hawaiian winter grounds. *Canadian Journal of Zoology* 80:1938-1947. 2002.
87. **Stafford KM, Fox CG, Clark DS.** Long-range acoustic detection and localization of blue whale calls in the Northeast Pacific Ocean. *Journal of the Acoustical Society of America* 104:3616-25. 1998.
88. **Stafford KM, Nieukirk SL, Fox CG.** An acoustic link between blue whales in the eastern tropical Pacific and the northeast Pacific. *Marine Mammal Science* 15:1258-1268. 1999.
89. **Stafford KM, Bohnenstiehl DR, Tolstoy M, Chapp E, Mellinger DK, Moore SE.** Antarctic-type blue whale calls recorded at low latitudes in the Indian and eastern Pacific Oceans. *Deep Sea Research Part I: Oceanographic Research Papers* 51(10): 1337-1346. 2004.
90. **Stevick PT, Allen J, Bérubé M, Clapham PJ, Katona SK, Larsen F, Lien J, Mattila DK, Palsbøll PJ, Robbins J, Sigurjónsson J, Smith TD, Øien N, Hammond PS.** Segregation of migration by feeding ground origin in North Atlantic humpback whales (*Megaptera novaeangliae*). *Journal of Zoology* 259:231-237. 2003.
91. **Suzuki R, Buck JR, Tyack PL.** Information entropy of humpback whale songs. *Journal of Acoustical Society of America* 119:1849-1866. 2006.
92. **Thompson PO, Findley LT, Vidal O, Cummings WC.** Underwater sounds of blue whales, *Balaenoptera musculus*, in the Gulf of California, Mexico. *Marine Mammal Science*. 12:288-92. 1996.
93. **Thompson TJ, Winn HE, Perkins PJ.** Mysticete sounds. In: *Behavior of Marine Mammals*, edited by Winn HE, Olla BL: Plenum, 1979.
94. **Tyack P.** Differential responses of humpback whales, *Megaptera novaeangliae*, to playback of song or social sounds. *Behavioral Ecology and Sociobiology* 13:49-55. 1983.
95. **Tyack P.** Interactions between singing Hawaiian humpback whales and conspecifics nearby. *Behavioral Ecology and Sociobiology* 8:105-116. 1981.
96. **Tyack P, Whitehead H.** Male competition in large groups of wintering humpback whales. *Behavior* 83:132-154. 1983.
97. **Tyack PL.** *Humpback whales respond to the sounds of their neighbours*. PhD Thesis, The Rockefeller University, New York. 1982.
98. **Valsecchi E, Hale P, Corkeron P, Amos W.** Social structure in migrating humpback whales (*Megaptera novaeangliae*). *Molecular Ecology* 11:507-518. 2002.
99. **Ward S, Speakman JR, Slater PJB**. The energy cost of song in the canary, *Serinus canaria*. *Animal Behaviour* 66:893-902. 2003.
100. **Watkins WA, Tyack P, Moore KE.** The 20-Hz signals of finback whales (*Balaenoptera physalus*). *Journal of Acoustical Society of America* 82:1901-12. 1987.
101. **Weinrich M.** Early experience in habitat choice by humpback whales (*Megaptera novaeangliae*). *Journal of Mammalogy* 79:163-170. 1998.
102. **Winn HE, Bischoff WL, Taruski AG.** Cytological sexing of cetaceans. *Marine Biology* 23:343-346. 1973.
103. **Winn HE, Perkins PJ, Poulter TC.** Sounds of the humpback whale. In: *Proceedings of the 7th Annual Conference on Biological Sonar and Diving Mammals*, edited by Poulter, TC: Stanford Research Institute, 1971.
104. **Winn HE, Winn LK.** The song of the humpback whale, *Megaptera novaeangliae*, in the West Indies. *Marine Biology* 47:97-114. 1978.
105. **Winn LK, Winn HE.** *Wings in the Sea: the Humpback Whale*. London: University Press, 1985.
106. **Zahavi A.** Mate selection - a selection for a handicap. *Journal of Theoretical Biology* 53:205-214. 1975.
107. **Zahavi A.** The cost of honesty (further remarks on the handicap principle). *Journal of Theoretical Biology* 67:603-605. 1977.
108. **Zahavi A.** The theory of sexual selection and some of its implications. In: *International Symposium of Biological Evolution*, edited by Delfino, VP: Adriatica Editrice, 1987.