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AN EVALUATION OF EVOLUTIONARY PROCESSES IN KILLER WHALES (ORCINUS ORCA)

Since the time of Darwin, evolution, both of traits which are genetically transmitted and of traits which are learned, has been a topic of considerable interest. Natural selection has been postulated to act at several different levels. Darwin looked at selection as maximizing individual reproductive success. However, later thought questioned how traits which lower individual fitness, such as altruistic traits, could arise (Trivers 1971, Axelrod and Hamilton 1981). The principle alternatives have been that selection acts at the level of the group (to maximize population fitness, Winne-Edwards 1962) or at the level of the gene (kin selection, Hamilton 1964). Wilson (1977) has explored the conditions under which these two models make the same predictions. He found that structured demes, populations consisting of many smaller trait-groups, could fill this role. To discriminate among these models, one must be able to evaluate the costs and benefits of behavioral acts, and interpret them in light of the degree of relatedness of the individuals involved.

Processes of the evolution of cultural traits, that is traits which are passed on from one generation to the next by imitation, are also subjects of considerable interest. Mundinger (1980) proposed a model of branching-reticulate evolution. He suggested that cultural evolution should parallel genetic evolution. For example, imitation would be the equivalent of reproduction; insight, invention copy error, etc. would be sources of new traits; psychological selection would result in differential preservation of cultural traits; meme flow would be equivalent to gene flow, and memetic drift should parallel genetic drift. Although Mundinger could not cite any examples of memetic drift, he suggested it would be found in small populations.

These ideas are drawn primarily from terrestrial observations. However, as general principles, they should apply to marine systems as well. A marine system which consists of small groups within larger groups and has cultural traits would be the most interesting to study, since it could be used to examine levels of selection, as well as the evolution of cultural traits.

Connor and Norris (1982) suggested that the odontocete cetaceans may have evolved reciprocal altruism. If this is correct, then odontocete schools could be used to examine levels of selection. For example, altruism could be analyzed to determine whether it is best explained by selection at the level of the gene (nepotism), individual (reciprocal altruism), or group.

Killer whales (Orcinus orca) are an excellent species for exploring these concepts. A killer whale is a member of several different trait-groups. The smallest of these is the mother-offspring group. Pods consist of one or more mother-offspring groups which normally travel together and use similar sounds (Bigg 1982; Ford and Fisher 1982, 1983). Pods which share some call types are termed acoustic communities (the vocal repertoires of these pods constitute the "institutions" of Mundinger). Pods which associate with one another are called communities (the "demes" of Wilson). Communities may be geographically separated (e.g., the northern and southern resident communities of British Columbia), or may overlap spatially (e.g., the transient community with the two resident communities: Bigg 1982). Thus a killer whale encounters both closely and distantly related individuals on a regular basis (from the same mother-offspring group and different pods, respectively), in addition to rare encounters with other distantly related individuals (from a different community). The occasional interactions between residents and transients may provide the structure required by Wilson's model. Thus the structure and behavior of killer whale populations contain the range of variation necessary for testing hypotheses about the process and rate of selection of genetical and cultural traits.

Bigg (1982, personal communication) has conducted long-term observations of wild killer whales. His study showed that all individuals in the Vancouver Island area are recognizable by the shape of the dorsal fin and saddle, a grey patch posterior to the dorsal fin. Mother-offspring relationships of calves born during the study period are known. By observing typical mother-offspring association patterns, he was able to identify the mothers of many other juveniles and sub-adults. Photographic records of juveniles at capture sites in the 1960's provide the relationships among some adults. He noted the absence of dispersal, that is, all individuals remained associated with a particular adult female throughout the study. Given the absence of dispersal, he suggested that pods are likely to consist of closely related individuals and that new pods may form by gradual separation of matrilines. His work has not revealed the mating system. The rate of new pod formation and the mating system are needed to determine degrees of relatedness.

Killer whale sounds were first recorded in the 1960's (Valdez 1961). Schevill and Watkins (1966) described screams composed of rapidly repeatedly clicks. Clicks consist of both high and low frequency components. Poulter (1968) found the screams could be placed in several discrete categories, and noted that two individuals used different repertoires. Steiner et al. (1979) described unstereotyped whistles (this is surprising, since many delphinids use stereotyped whistles: Caldwell and Caldwell 1965; Caldwell, Caldwell and Hall 1973; Steiner 1981). Jehl et al. (1981) and Awbrey et al. (1982) noted macrogeographic variation among the North Atlantic, North Pacific, and Southern Ocean.

Ford and Fisher (1982, 1983) reported stable dialects in killer whales. The dialects are composed of different repertoires of discrete calls. They further noted that how often pods were seen together was an indicator of the similarity of their sound production. They suggested that the overlap of dialects could be used to estimate the relatedness of pods. As with new pod formation, information on the rate of dialect formation is unavailable.

Dahlheim and Awbrey (1982) were able to discriminate individual captive killer whales by sound. This suggests variation in call structure at the individual level. Evidence that call structure is learned is tentative and comes from observations of killer whales in captivity. Bain (1984) noted that calls produced by an Icelandic killer whale had become very similar to those of a tank mate from British Columbia, in contrast to those used before they were placed together. This suggests that variation exists and may be learned by imitation, the necessary conditions for cultural evolution to occur.

Work to date is nearly sufficient to begin examining levels of selection and rates of cultural evolution in this species. The missing data are: relatedness of adults within a pod, the patrilineal contribution to degrees of relatedness, and variation in vocal behavior as a function of relationship. This project is intended to fill in these gaps.

Objectives of the Study

The objectives of this study are: 1) to determine the matrilineal relationship of adults within a pod; 2) to determine the mating system in the population, and hence degrees of relatedness; 3) To determine the structure of vocalizations of individuals whose relationships to each other are known; 4) to use this information to produce a model for pod formation; and 5) to use historical reconstruction to examine the evolution of vocal behavior in the population.

Study Area and Animals

The population to be studied is resident to Northern British Columbia (the northern resident community, Bigg 1982). Over the last three summers, members of this population have been observed on over 90 % of the days in Johnstone Strait. The sheltered waters in this area make it ideal for research. Past studies and the availability of captive animals from this population offer additional advantages for research in this area.

Matrilineal Relationships Based on Surface Association

The relationships of most whales in the population are being determined by Bigg (personal communication) based on photographs of whales at the surface at the same time. However, a few whales are not expected to fit the mother-offspring pattern. These whales are postulated to be grandmothers, aunts or uncles, but determinations within these categories do not appear to be possible using association alone (S. Heimlich-Boran, personal communication).

A more detailed approach to the question of surface association is to record respiratory sequences. It appears that mothers normally surface prior to their offspring. In the cases of adults which were photographed as juveniles during capture operations, this appears to be the case as well. The persistence of this pattern into adulthood might prove effective for determining matrilineal relationships among adults.

Mating System and Patrilineal Relationships Based on Morphology

The mating system of killer whales has been difficult to determine for several reasons. First, mating is believed to take place during parts of the year when weather does not permit observation. Copulations which take place underwater or at night would be difficult or impossible to observe. Finally, even if copulations were observed, many cetaceans copulate when they are not in breeding condition (Caldwell and Caldwell 1977), so these may not be effective.

An alternative approach is to look for genetic signatures (Beecher 1982, Wu et al. 1980). Evans et al. (1982) noted variation in the color pattern of killer whales throughout the world. Many of these variants can be observed in the northern resident community. By understanding the genetics of color patterns and other morphological traits, one should be able to describe the possible appearances of fathers.

Photographs of saddles, dorsal fins, and post-ocular patches have been examined and placed in various categories. The second step is to determine inheritance rules, e.g., describing traits as dominant, recessive, or incompletely dominant. Then these rules can be tested for logical consistency (e.g., no offspring should be homozygous for a trait its mother does not possess). To test the validity of the model, the probability of it fitting the data by chance will be determined. For example, a female heterozygous for several traits crossed with an unknown male could produce just about any kind of offspring. But, even if 90 % of possible patterns could be produced, a sample of 30 mother-offspring pairs would be sufficient to test to the $p < .05$ level. An additional test, to avoid the circularity of testing the data set used to produce the rules, would be to test them on a different population, such as the southern resident community.

Then offspring could be compared to their mothers to determine what their fathers would have looked like. This could identify some fathers, and their matrilineal relation to the mother could be used to describe the mating system. This would provide the patrilineal contribution to degrees of relatedness, which will yield the average degree of relatedness of various classes of individuals.

(In the future, collection of tissue samples from selected individuals for chromosome analysis (Arnason et al. 1980) or isozyme analysis Duffield (1984) could be used to confirm findings concerning degrees of relatedness and the mating system.)

Structure of Vocalizations as an Indicator of Matrilineal Relatedness

The principal focus of this study is to record calls from known individuals and families. This task consists of three major components: developing a method for localizing underwater sound; developing a measure of the similarity of vocalizations; and data acquisition and analysis.

Localization of Underwater Sound

Studies of underwater acoustic signals have been hampered by the inability to identify signal sources. Two basic approaches are used to determine the source. The first is amplitude measurement. Loud sounds sometimes can be attributed to the animal nearest the hydrophone. Measuring arrival-time (or phase) differences along a hydrophone array is another approach. Signals are recorded on different channels of a tape recorder and then lined up to determine arrival-time differences. These time differences are then used to calculate source location.

Various array sizes have been tried. Large arrays (e.g., Watkins and Schevill, 1971, 1972, 1974, 1977, and Watkins 1976) are more precise at long distances provided arrival-time differences are accurately measured, but signals are subject to more distortion and large vessels are required to deploy them. Small arrays (e.g., Clark 1980) are useful primarily for determining direction, but can produce fair estimates of distance when arrival times are accurately measured.

The method used here is to deploy a three-meter tetrahedral array. This produces a maximum separation of 2 msec (i.e., it takes 2 msec for sound to travel from one hydrophone to another). The signals from the array are recorded on an HP 3968A eight-channel tape recorder. Two channels are stored simultaneously in an HP 5451C Fourier Analyzer System. The cross-correlation function of the machine is used to measure the arrival-time difference between these two channels. By using the tape-servo function, playback times should be accurate ± 5 microseconds. Additional errors, such as noise, tape drop-outs, doppler shifts, non-linearities in the ocean, and variance in the frequency response of different channels of the recording system will also affect the accuracy of time-difference measurements. When an overall accuracy of 20 microseconds (1 %) can be attained, direction to the source can be determined within a few degrees, but distances will be known rather imprecisely. This level of accuracy is about the same as that obtained when noting the location of a whale visually.

The Similarity of Sound

Many methods have been used to classify animal sound (e.g., Hafner et al. 1979, Dahlheim and Awbrey 1982, Miller 1979, Martindale 1980 ab, Clark 1982). However, these are often based on what the observer considers to be artificial categories (Clark, personal communication; Miller, personal communication). While a "natural" method is not feasible at present (Miller 1979), one based on models of biological information processing may prove more satisfactory than those based on features which are easy to measure.

It appears that models of the visual system are generally much better developed than those of the auditory system. This is not necessarily a problem, since one can classify sounds by looking at spectrograms (Slater et al. 1984) and the various sensory modalities are likely to function in a similar manner (see Puccetti and Dykes 1978, Bridgeman 1978, Bach-y-Rita 1972, and Bain 1983).

The method under development stems from the spatial frequency theory of vision (Campbell and Robson 1968, Campbell 1977, Robson 1983, Daugman 1980, Pollen and Ronner 1981). A computer model of this type of processing has been developed by Watson (1983). Modifications of this model based on the auditory literature (e.g. Dolmazon 1982, Moller 1982) and the observed structure of killer whale calls are being used in an effort to classify sounds by recursive application of Fourier analysis. The basic approach is to calculate the frequency structure of a call. The call is then split into frequency bands, and the power spectrum of the change in power through time of each band is determined. The power spectra of the power spectra are compared to determine the similarity of sounds.

By examining the variation between mothers and their offspring, one would find a measure of the amount of change likely to occur in one generation. By examining the variance among offspring of particular females, one would find a limit on how much variation there could be between sisters. These findings would permit a second test of the relatedness of adult females within a pod.

Data Acquisition

The research group will camp on West Cracroft Island, British Columbia, from late June to early September, 1985. When killer whales are located by shore-based observers, they will be approached in an 18' fiberglass motor boat. The individuals will be identified and the hydrophone array placed in front of them. Their locations will be recorded as they pass the array. The array is then moved and the process repeated. Identifications will be visual, but photo documented when possible. Photographs obtained in these settings may be used for morphological analysis, and surfacing sequences of whales passing the boat may be used in the respiratory sequence analysis.

Data Analysis

Data will be analyzed at the Marine Acoustic Services Laboratory of the University of California at Santa Cruz during the academic year following the field season. Equipment available includes an HP 5451C Fourier Analyzer System for sound analysis and computer facilities for additional data analysis.

Models of Pod Formation

Two models seem likely to describe pod formation. A deterministic model would state that it is part of the normal life-cycle of a female to form a new pod. Females which failed to raise female offspring would lead to dead ends, so on average the number of pods would remain constant. Alternatively, new pod formation could be a rare event. New pods would only form at times of ecological opportunity, such as the opening of new habitat or following the mass stranding of another pod (Bigg, personal communication).

These two models make different predictions about the relatedness of reproductive females within a pod. Under the first model, they would be closely related, normally sisters or cousins. Under the second, they could be distant cousins, or as close as sisters. These models would be supported by finding that individuals within a mother-offspring group sound more like each other than other individuals within the same pod. They could be discriminated between by the relatedness found for reproductive females within a pod.

Other models, such as merging of maternal subgroups, or coalescence of unrelated males and females, seem unlikely, since these events have not been observed (but see Balcomb et al. 1982). However, longer term observation may reveal reticulate pod formation.

Historical Reconstruction

Historical reconstruction is a method which attempts to describe unknown ancestral forms based on extant forms (Platnick and Cameron 1977, Goodman et al. 1978). To do this, forms which are identified as functional equivalents (e.g., two words with the same meaning or different forms of the same protein) are compared. Characters which are the same in all extant forms are assumed to be the same in the common ancestor. Characters which vary are assumed to have the form which is most common in the extant population. These ancestral forms, in turn, may be compared, and a prior ancestor reconstructed. While the confidence one has declines with each extrapolation, one also gets an impression of which forms have a common ancestor, and how far back in time divergence occurred. Genetic traits which can be traced in this manner are called "homologous traits," and cultural traits are called "institutions" (Mundinger 1980).

The final step of this project will be an historical reconstruction of call types. Using the model for pod formation, and the amount of change found between generations, the age and structure of ancestral forms of calls will be estimated. This reconstruction may reveal whether the study area was colonized once or many times since the last ice age (Bigg, personal communication), and the timing of colonization.

Value of the Research

Once degrees of relatedness are known, they can be used in conjunction with studies of the natural history of the species to examine the process of selection. Examples of such studies in progress by other workers include: foraging strategies (Felleman and Heimlich-Boran, Jacobsen and Gallagher), reproductive behavior (Bigg), and social organization (Bigg, Balcomb, Osborne, Heimlich-Boran) These could be analyzed in terms of costs, benefits, and degrees of relatedness.

Determining the pattern of new pod formation would provide new data for theories on dispersal (the absence of dispersal is rare in birds and mammals; Greenwood 1980; so the killer whale pattern should prove very instructive).

A portable system for localizing underwater sound will be valuable in future studies of cetaceans. Continued study of known individuals could be used to describe the development of vocal behavior. Sound sequences from individuals would be valuable in efforts to understand communication. An automated technique for classifying sounds would be quite useful in such studies.

Summary

This project, using behavioral and morphological techniques, will determine degrees of relatedness within a population of killer whales. By examining differences in vocalization, a cultural trait, and determining the time over which these differences may have arisen, an estimate of the rate of cultural evolution will be obtained. This information will be valuable in evaluating theories concerning evolution.

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