A neglected science: applying behavior to aquatic conservation

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Synopsis

Behavioral theories, insights, and techniques are too frequently ignored by conservation biologists. Yet an animal's survival and reproductive success clearly depend on its behavior. Using examples from marine, freshwater, and terrestrial realms, I assert that behavioral information is invaluable in five conservation areas: (1) managing wild species (e.g., designing marine reserves; reducing animal–human conflicts; understanding and managing species' responses to human-induced environmental stress such as fishing, introduced species, and chemical, visual, and acoustic pollution); (2) actively reversing the decline of imperiled wild species (e.g., reducing bycatch by improving selectivity of fishing gear; re-establishing breeding populations and boosting reproduction); (3) assessing biodiversity (e.g., modeling population viability; censusing and monitoring populations and species); (4) captive breeding and reintroduction programs (e.g., minimizing loss of valuable phenotypes; teaching or maintaining valuable survival skills); and (5) changing human behavior in resource exploitation (e.g., using principles from social psychology). Both realized and potential applications to fishes are stressed. Finally, behavioral diversity, a valuable but neglected element of biodiversity, needs to be explicitly conserved to maintain diverse populations. Arguments are presented that the conservation of species diversity and genetic diversity alone does not necessarily protect important behavioral diversity. The maintenance of both individual and population variability may be essential for the preservation of a species.

Introduction

Ultimately, it is behavior that determines survival
Timberlake & Lucas 1989, p. 249
Natural selection operates on behavioral outcomes
Vaccarino et al. 1989, p. 130

Over the years, we have come to recognize the need for conservation efforts to incorporate knowledge from ecology, population genetics, sociology, anthropology, and economics. However, one field of study, behavior, is still neglected. Three widely-used conservation biology textbooks (Soulé & Wilcox 1980, Soulé 1986, Primack 1995) include just two chapters among them with some discussion of behavior, primarily related to captive-breeding issues. I surveyed behavior as a key word in the journal Conservation Biology for the years 1993–1997. Only 38/550 papers (7%) of the papers mentioned behavior. Only 4 (0.7%) addressed fish behavior.

Why is behavior so important? As the above quotes emphasize, how an animal behaves determines its survival and reproductive success. Hence, behavior affects population structure and demography, as well as community structure. Neglecting behavior can lead to the failure of particular conservation practices. For example, sea turtle nests are routinely relocated to boost the number of surviving hatchlings. Recent behavioral studies have indicated the relocated sites should not be surrounded by low-lying vegetation, as hatchlings move away from dark objects and consequently do not move toward the ocean (Godfrey & Barreto 1995, Godfrey 1996). Conservation efforts need to include behavioral information to ensure that management practices make sense in the animal's world.

In this paper, I argue that both animal and human behavior have important applications to conservation biology. Behavioral fields of obvious and potential importance to conservation include ethology, neuroethology, behavioral ecology, sensory physiology, psychology, and cognitive studies. Just as neuroscience has made tremendous advances by incorporating research at all relevant levels from the molecular to the psychological, so too will conservation biology advance by incorporating information on individuals, populations, species, and co-existing species. Behavioral fields can provide valuable contributions at all of these levels and should therefore be an integral part of conservation biology.

I would like to emphasize three main points: (1) Population survival depends on behavior across the continuum of heritable and environmental influences, including learned, imitative, and adaptive behavior. (2) Behavioral diversity, a valuable and neglected element of biodiversity, needs to be explicitly conserved. Currently, biodiversity is defined as encompassing genetic, species, and ecosystem diversity: the term should be redefined to include behavioral diversity as well. As argued in the following section, a focus on the other levels of diversity does not adequately conserve the diversity of behavior. (3) Behavioral methods, techniques, and insights can enhance the success of conservation practices. To explore these three areas, I will draw on examples of how individuals, social groups, and populations interact with the environment and each other. Some of this information has already been applied to the conservation of fishes; some examples come from the literature on the conservation of birds or terrestrial mammals, but should also be applicable to fishes; and some examples are the results of basic research that, although speculative, may be useful in conservation.

Why behavior has been neglected

Part of the reason for behavior's neglect is historical: the fields of ecology and population genetics have dominated conservation biology, and behavioral biologists and other behavioral scientists have not been particularly vociferous in asserting their role. Second, in assessing species diversity, taxonomists have largely ignored behavioral traits in identifying species (Buchholz & Clemmons 1997). Third, only recently have behavioral scientists recognized that individual behavioral variation influences population and community dynamics. Fourth, conservationists have failed to recognize what neuroscience, ethology, and behavioral ecology are telling us: brains and behavior are extraordinarily plastic. Much behavior thought to be exclusively hard-wired is now known to be learned or otherwise environmentally determined to some degree (Barlow 1991, Normile 1998). These determinants must be provided or the behavior cannot be elicited or maintained.

Stereotyped, heritable behavioral traits can help sort out phylogenetic position. Behavioral phylogenies are similar to those derived from morphology (e.g., Kennedy et al. 1996, see also Johnston 1999 this issue). The identification of biological species and evolutionarily significant units among the cichlid flocks in the African Great Lakes is facilitated by the use of behavioral studies together with morphological and genetic analyses (Stauffer et al. 1995, Seehausen et al. 1997).

Behavioral studies have helped identify multiple species where only one was previously recognized based on morphology alone. A study of the vocalizations of the nocturnal primate, the bushbaby, *Galago* spp., identified at least ten to possibly 34 new species previously missed because of similar morphologies (Zimmerman et al. 1988, Bearder 1995). Similar discoveries have occurred in fishes, insects, birds, and other mammals (Buchholz & Clemmons 1997). Because behavioral traits are generally not used to assign taxonomic ranking, '... functionally valuable variation in behavior is not likely to be protected under present classification schemes' (Buchholz & Clemmons 1997, p. 190). In neglecting behavioral diversity, we underestimate species number and thus underestimate the rapid rate of species extinction.

Maximizing genetic diversity may not adequately conserve behavioral diversity

Traditionally, conservationists have focused on population genetics, assuming that maximizing genetic diversity would also conserve behavioral diversity. Some researchers have even suggested that conservation should target overall genetic heterozygosity or heterozygosity at certain loci (Hughes 1991, Miller 1995). Recent studies, however, indicate that maximizing genetic diversity as a conservation practice will not automatically maintain behavioral diversity in and of itself. Why?

There is a nonlinear relationship between genotypic diversity and phenotypic expression. Large changes in gene frequency can occur with minimal adaptive value (Buchholz & Clemmens 1997). Conversely, a few genotypic differences can make disproportionately large phenotypic differences, such as with homeotic selector genes which determine the specificity of developing segments in *Drosophila*. Similar genes have been found in almost every animal studied (Powell 1997).

A population can include members with different behavioral genotypes, or alternatively, different behavioral phenotypes. A single genotype can generate two or more discrete phenotypes, each with a unique ecological or social role (Stearns 1989). Alternative reproductive phenotypes are common in fishes (Chan & Ribbink 1990, Shapiro 1991, reviewed by Brantley et al. 1993). The midshipman, *Porichthys notatus*, has two different male morphotypes with different reproductive styles. One courts females acoustically in its territory; the other is a sneaker (Brantley et al. 1993).

Also, current measures of higher-order genetic diversity do not necessarily reflect local population-specific genetic adaptation. Buchholz & Clemmons (1997) cite the nest-maintenance behavior of honeybees, which is critical in protecting against disease, yet controlled by only two genes (Rothenbuhler 1964). In the case of fishes, population-specific genetic adaptations of the guppy, *Poecilia reticulata*, against predators (Magurran et al. 1993) or life-history differences between chinook salmon, *Oncorhynchus tshawytscha* (Hedgecock et al. 1994) are similarly not detectable with current genetic techniques. Local genetic adaptation becomes increasingly important for population survival, given the rise in habitat fragmentation in both aquatic and terrestrial landscapes.

The ability of current genetic methods to detect behavioral diversity is of immediate concern to governmental agencies such as the United States Fish and Wildlife Service (USFWS) and the National Marine Fisheries Service (NMFS) as they attempt to define 'evolutionarily significant units' under the Endangered Species Act (ESA) (U.S. Dept. of Interior et al. 1996, p. 4722). Current policy considers population segments unique only if there are demonstrated 'quantitative measures of genetic or morphological discontinuity' (Pennock & Dimmick 1997, p. 616). Only fourteen percent of the groups currently protected as distinct population segments under the ESA would qualify under this more stringent definition. Behavioral justifications for preserving particular populations would be excluded from consideration if the behaviour cannot be shown to be heritable with existing molecular genetic techniques to analyze the structural genome (Behnke 1995, Pennock & Dimmick 1997). A better definition of the term 'evolutionarily significant unit' is needed to preserve adaptive variability in populations, including variability in behavior.

Behavioral variability has manifold origins

Developmental experience, social conditions, and parental or conspecific learning all play a part in generating behavioral variability. Social systems themselves can be plastic, changing as a result of changes in food, habitat size or quality, or population density. In some situations, social situations will predictably change for a given species in response to environmental change; there also can be intraspecific differences in social systems, both intra- and inter-site (Lott 1991, Shapiro 1991). McNicol & Noakes (1984) showed that juvenile brook charr, *Salvelinus fontinalis*, can switch rapidly from dominance hierarchies to individual territories to schools, depending on their social and physical environment. Within a social structure, what an individual perceives, does, and becomes can depend on its social interactions with neighbors (reviewed by Lott 1991; primates Sapolsky 1987; fish Fox et al. 1997, Winberg et al. 1997).

Learned behavior can be critical for population survival

Studies on a number of species, including fishes, have shown the importance of learning in predator avoidance (Verheijen 1956, Smith & Smith 1989, Mathis

et al. 1996), habitat choice (Kramer et al. 1997), long distance migration (Dodson 1988, 1997), food preferences (Bilkó et al. 1994), mate choice (Wade & Pruett-Jones 1990, Brooks 1996), selection of spawning sites (Warner 1988, Shapiro 1991), and daily foraging routes (Helfman & Schultz 1984). Warner (1991) argued that coral reef fishes, in particular, should exhibit high phenotypic plasticity in behavior, given pelagic dispersal of embryos and larvae and the considerable environmental and social variability of a reef environment.

Helfman & Schultz (1984) showed that French grunts, *Haemulon flavolineatum*, use social learning to pass on their knowledge of daytime schooling sites and twilight migration routes. The social characteristics of grunts that led to prediction of social transmission are found in other marine fish species. These include traditional schooling sites, consistently used, precise migration paths, and overlap in age cohorts, essential for socially transmitted behavior.

Some behavior such as kin recognition and habitat- and sexual-imprinting are learned only during a sensitive period of development and cannot be learned later (Myers et al. 1988). Coho salmon, *Oncorhynchus kisutch*, need to learn an odor sequence during their seaward migration in order to home to the correct river system when they return to spawn (Quinn et al. 1989). The sequence depends on the timing at which the fish experiences given locations and the physiological state of the fish at that time (Pascual & Quinn 1995).

Adaptive changes in individual behavior can be increasingly important for wild species when confronted with an introduced exotic. Buchholz & Clemmons (1997) noted the importance of a change in nesting site by endangered Mauritius kestrels following the invasion of macaques. The traditional tree-nesting site of the kestrels was readily reached by the macaques, and the population was decimated. The species rebounded after a pair of kestrels began nesting on cliffs inaccessible to the monkeys. Given the widespread introduction of exotic fishes worldwide and their documented impacts on native species (e.g., Moyle & Leidy 1992), it would be useful to determine if native species surviving such introductions were capable of analogous shifts in breeding behavior or other types of behavior, such as shifts in feeding or predator avoidance.

Behavioral diversity needs to be explicitly conserved

To maintain diverse populations, behavioral diversity, like genetic and species diversity, must be explicitly conserved. Therefore, behavioral diversity should be an integral part of the definition and measurement of biodiversity. At the moment, individual and population variability in behavior that may be essential for the preservation of species is neglected, threatening both survival and the potential for evolutionary change (Dingle et al. 1997). The stability of populations can be affected by individual variability in reproductive behavior, dominance, and spatial distribution (Magurran 1993). Behavioral diversity at the population level has relevance for aquatic conservation given that: (1) reserves and parks protect populations, not species; and (2) a number of aquatic species are believed to have metapopulations (Doherty 1991).

Part of this behavioral diversity is learned. Cultural traits evolve more rapidly than the genome can track and may be more rapidly lost by selective extinction. While it is possible that cultural traits can also be restored by human intervention, the process can be difficult. A population of trumpeter swans lost their migratory knowledge because the older swans were killed before the young could acquire the trait. Extensive and costly human intervention was necessary to attempt to restore the behavior (Baskin 1993). Many pelagic fish species, including imperiled species such as bluefin tuna, *Thunnus thynnus*, engage in large-scale migrations. Selective harvest of larger fish could have analogous consequences for the maintenance of these populations if the migratory pattern depends on cultural transmission across age cohorts.

Behavioral diversity also merits conserving due to its scientific value in speciation theories, comparative neuroscience, and other aspects of evolutionary theory. The extraordinary behavioral plasticity of fishes is believed to contribute partly to their evolutionary success as a group (Godin 1997). Behavioral patterns among populations of coral reef fishes can be useful in determining the rate and direction of evolution (Warner 1991). The behavioral diversity found in species of cichlids from the African Great Lakes has contributed greatly to an understanding of the role that sexual selection plays in evolution (McElroy & Kornfield 1990, McKay 1991).

Further, if we are truly interested in conserving representative aspects of Earth's fauna, unique and/or evolutionarily critical behavior patterns – what Brower & Malcolm (1991) call endangered phenomena – should be saved. In other words, *phenomena* as well as species should be saved. A terrestrial example is the spectacular migration of monarch butterflies en masse to Mexico: while the species is not at risk, these migrations are (Buchholz & Clemmons 1997). Fishes display a wealth of fascinating behavior patterns worthy of preservation. Unique behavior such as mass spawning aggregations, culturally transmitted behavior, or singular behavioral phenotypes or genotypes should be conserved even if the species itself is not at risk.

Applying behavioral methods, techniques, and insights to conservation

Broadly, understanding behavior is particularly relevant to five areas of emphasis in conservation biology: (1) managing wild populations; (2) actively reversing the decline of endangered wild species; (3) assessing biodiversity; (4) captive breeding and reintroduction; and (5) changing human behavior associated with resource exploitation.

Managing wild populations

Although applications of animal behavior to management have been limited, they have great potential (Curio 1996). A common goal of management is to increase or decrease the size of a given population. This goal can be facilitated by identifying behavioral factors regulating population growth, such as how a social system varies with resource availability or stress (Parker & Waite 1997). Indication of behavioral disturbance as a result of resource exploitation (e.g., disturbance of feeding, change in habitat or locomotor activity, hormonal response to stress, change in social system) can also be a useful monitor of stress on a species before reproduction is affected (reviewed by Hontela et al. 1993, Smith & Logan 1997, Wingfield et al. 1997).

Behavioral insight can be important in assessing the design of and even the merits of a particular conservation practice. An increasingly common practice is translocation: moving wild individuals to other sites to reestablish or increase a population (Griffith et al. 1989, see Rakes et al. 1999 this issue). Male elephants translocated as orphans from culled groups to other parks in South Africa developed disturbed social behavior and killed 30 white rhinos in three years. This seemingly inappropriate aggression was thought to result from lack of social guidance from other males when the orphans were young (Bartlett 1997). Thus, using the orphans to reestablish herds elsewhere backfired due to the conservationists' lack of understanding of elephant social behavior. Now entire elephant families are moved instead. The failure of hatcheries to reestablish populations of endangered salmon can similarly be attributed in part to a lack of behavioral understanding (Meffe 1992). Hatchery practices have been directly blamed for a ten-fold reduction in wild spawner densities of coho salmon over the last 30 years (Flagg et al. 1994); these practices include selection for early spawning, making the fish maladapted for establishing self-reproducing populations.

Designing marine reserves

Although the science of marine-reserve design lags behind that of the design of terrestrial reserves, in both cases the behavior of pivotal animals should influence the design. Why? Ignoring behavior can affect the success of the conservation effort. For example, while many Central and South American bird reserves are often restricted to mountaintops, an understanding of the behavior of the local birds would have shown that 25% of the birds leave the protected area to forage in lower areas (Beissinger 1997).

In determining the size, shape, location, and habitats of a marine reserve, information on recruitment and settling; spawning, resting, and foraging habitats; territorial ranges; and daily and seasonal patterns of migration are all important for maximum conservation success (see Beets & Friedlander 1999, Kramer & Chapman 1999, Tupper & Juanes 1999, and Wolff et al. 1999, all this issue). Here too, population variation is important: species widely distributed at one site may not be so distributed at others (Williams 1991). Fishelson et al. (1987) showed that the behavior of the surgeonfish, *Acanthurus nigrofuscus*, differed dramatically between two sites less than 2 km apart! At one site, feeding migrations occurred to an area 400 m away; at the other, no feeding migrations occurred.

Recruitment.– Settlement of coral reef fishes was thought to be passive and random. We now know that the larva period of fishes is behaviorally complex, and that both behavioral and stochastic factors play a role. Distributions of larvae are affected by six factors, the

first four of which are behavioral: (1) adult spawning location and timing; (2) vertical distribution of larvae; (3) horizontal swimming by larvae; (4) behavioral capabilities and flexibility of larvae; (5) hydrography; and (6) topography (Leis 1991). Some fishes can extend their larva period if they don't encounter suitable habitat, and post-settlement habitat shifts can occur as well (Kaufman et al. 1992, Kramer et al. 1997). The influence of recruitment on population structure will be greatest for those species with low post-settlement mortality, such as some damselfishes (Williams 1991).

Habitat selection.– The behavior of animals clearly influences their choice of habitats and the spatial extent of their habitat requirements. Environmental and social variables important for fish habitat selection include the physical and chemical characteristics of the water, characteristics of the substrate, and the presence or absence of conspecifics or other species (Kramer et al. 1997). On coral reefs, depth and substrate type are important environmental factors (Luckhurst & Luckhurst 1978). Many species use the presence or absence of conspecifics (Sweatman 1983, Jones 1987, but see Doherty & Williams 1988) as well as other species (e.g., prey, predators, or competitors) as criteria influencing habitat selection (Reed & Dobson 1993, Jordan et al. 1997, Kramer et al. 1997).

Social organization can increase the size of a home range beyond that predicted by body size alone, particularly for species with complex social systems (Komdeur & Deerenberg 1997, see Kramer & Chapman 1999 this issue). Hence an understanding of social organization is critical for adequately protecting a given population. Shapiro (1987) showed that different types of social groupings of the serranid fish, *Anthias squamipinnis*, have home ranges of different size. These different types of groupings can occur within the same population (also see van Rooij et al. 1996 for scarids).

Numerous fishes utilize different habitats at different periods of their lives. These habitats may all need protection if a species is endangered or overexploited. In some species, however, an effective marine reserve may possibly be achieved simply by protecting mass spawning sites. Beets & Friedlander (1999 this issue) showed that overfished stocks of the red hind, *Epinephelus guttatus*, can recover simply by closing the spawning area to fishing during these periods.

Increasing habitat fragmentation can prevent movement among populations within a metapopulation, leading to local extinctions (Meffe 1995). At what distance does movement stop? The answer depends on an animal's willingness to relocate across gaps, which depends on knowledge of its *perceptual range of habitat selection* (reviewed by Lima & Zollner 1996; birds Desrochers & Hannon 1997; mammals Wolff et al. 1997). In other words, at what distance can an animal detect a desirable habitat or patch? Psychophysicists and sensory physiologists can help identify the dominant sensory cues an animal utilizes in deciding to relocate to another habitat. What is the conservation significance? Animals with a broader range may be more likely to leave their home if they are able to find other suitable habitat quickly. In contrast, animals with a limited range may be more reluctant to leave a fragmented site, due to the increased time and risk involved in looking for another suitable site (Lima & Zollner 1996). A study of the patterns of movement of six reef fish species indicated that a natural habitat boundary of sand between reefs prevented movement to adjacent reefs (Barrett 1995).

Species assessments.– As a diurnally-active species, humans tend to overlook nocturnally active species, which can bias measurements of species diversity on coral reefs and in other habitats. We need to take into account the vast number of nocturnally-active species and their habitat requirements when designing marine reserves and selecting potential sites for such reserves. Helfman (1993) has shown that one-fourth to one-third of the species in most fish communities are nocturnal and one-tenth are crepuscular (active at dusk and dawn). The twilight and nighttime activity areas of these species often differ from their daytime resting sites, requiring protection of larger and more diverse reef zones (see also Wolff et al. 1999 this issue).

Reducing animal–human conflicts
Minimizing animal-human conflict can engender local support for conservation actions. Behavioral manipulations can be used to repel animals from particular locations, such as sites for driftnets, busy harbors, hydroelectric dams, power generating stations, etc. A number of aquatic species have been shown to avoid particular frequencies and/or intensities of sounds (fishes Dunning et al. 1992, Knudsen et al. 1994; marine mammals Richardson et al. 1995; marine turtles O'Hara & Wilcox 1990, Moein et al. 1993). Acoustic repulsion devices have been used to generate avoidance responses in alewife, *Alosa pseudoharengus*,

near a power plant (Ross et al. 1993) and blueback herring, *Alosa aestivalis*, near dams (Nestler et al. 1992). The frequency of the sound matters. For blueback herring, only high-frequency sounds elicited an avoidance response; low-frequency sounds elicited a short-term startle response (Nestler et al. 1992). Strobe lights and air-bubble curtains have also been explored as methods of impingement mitigation (Zweiacker et al. 1977, Sager 1987).

On a speculative note, both classical and instrumental conditioning could help achieve a particular management goal (McLean 1997). Conditioning could be used to generate appropriate behavioral responses that have been lost in an imperiled species or to elicit inappropriate responses to reduce the numbers of an exotic species. Conditioning has been used to enhance predator avoidance in hatchery-reared coho salmon. Live predators and predation-associated stimuli were used to train the salmon to avoid lingcod, *Ophiodon elongatus* (Olla & Davis 1989).

Mitigating human-induced environmental stress
A knowledge of behavior can help in predicting a species' vulnerability to human-induced environmental change and in mitigating any resulting stress. Dubs & Corkum (1996) analyzed competitive interactions between an indigenous species of the U.S. Great Lakes, the mottled sculpin, *Cottus bairdi*, and an introduced species, the round goby, *Neogobius melanostomus*. Laboratory studies suggested that the more aggressive round goby will force mottled sculpins to leave their nearshore habitat for deeper habitats, where the sculpin have less food, fewer spawning sites, and are more susceptible to larger predators. The authors predicted that the introduced species will likely cause the demise of mottled sculpins.

Behavioral tests can also provide a noninvasive means of assessing the biological effects of anthropogenic environmental change. Swimming behavior, foraging behavior, and antipredator responses of fishes have been used in ecotoxicological assays (Lorenz et al. 1995, Kislalioglu et al. 1996, see Weis et al. 1999 this issue).

Pollution.– Chemical pollution can affect reproduction, feeding behavior, swimming, activity rhythms, territoriality, memory, orientation, settlement of larvae, and even predator-prey relations for those species dependent on chemical stimuli to locate prey (Sweatman 1988, Smith & Logan 1997, Weis et al.

1999 this issue). The olfactory mucosa of fishes can be damaged by various toxins (Blaxter 1988, Winberg et al. 1992).

Light pollution is also a problem. Sea turtles, other migratory species, and nocturnal aquatic animals can be profoundly affected by artificial lights which misinform the animal about correct orientation and alter the environmental periodicity of diel swimming patterns, migrations, and reproductive behavior (Witherington 1997). Given knowledge of the sensory physiology of the animal, light pollution can be managed effectively with such techniques as adjusting the light during critical times, altering light spectra, and reducing light duration (Witherington 1997).

Eutrophication can also affect both the quality and quantity of light in aquatic habitats and in turn influence visually-guided behavior such as those used in reproduction. Seehausen et al. (1997) documented a startling change in cichlid species diversity in parts of Lake Victoria after eutrophication. In comparing various sites around the lake, the researchers found a significant positive relationship between species diversity and light spectrum diversity, which was attributed to the effects of light quantity and quality on visually-guided mate choice. Similar research should be conducted on vision-dependent reef fishes in eutrophied areas or in areas with a high sediment load. A loss of discrimination ability may promote hybridization (Pyle & Randall 1994).

Humans have also altered the underwater sound environment, particularly in the low-frequency range (<200 Hz) (reviewed by Green et al. 1994, Richardson et al. 1995). The noise from ships, offshore oil drilling, and other sources can potentially affect the foraging, courtship and navigation of marine mammals, and lead to the avoidance of critical habitats (Richardson et al. 1995). Migrating gray whales avoided areas around offshore oil drilling when sound levels reached approximately 120 dB re: 1 μPa sound (calculated received levels) (Malme[1,2]).

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[1] Malme, C.I., P.R. Miles, C.W. Clark, P. Tyack & J.E. Bird. 1983. Investigations of the potential effects of underwater noise from petroleum industry activities on migrating gray whale behavior. Rep. 5366, Bolt Beranek & Newman Inc., Cambridge, MA for U.S. Minerals Management Serv., Anchorage AK. NTIS PB86-174171.

[2] Malme, C.I., P.R. Miles, C.W. Clark, P. Tyack & J.E. Bird. 1984. Investigations of the potential effects of underwater noise from petroleum industry activities on migrating gray whale behaviour/Phase 2: January 1984 migration. Rep. 5586, Bolt

Studies on acoustic pollution in fishes have been extremely limited, focusing primarily on examination of the sensory damage caused by intense sound (e.g., temporary thresholds shifts, hair cell damage) and laboratory studies of the masking effects on sound detection (reviewed by Fay 1988, Myrberg 1990, Hastings et al. 1996). However, we know that sound is used in a variety of fish behavior, including courtship and mating, and may be an important component of mate choice (e.g., pomacentrids, see Myrberg et al. 1986, Lobel & Mann 1995). It therefore seems plausible to speculate that acoustic pollution, like light pollution, could reduce selectivity in mate choice.

Fishing.– Worldwide, fishers have used their knowledge of fish behavior to catch fish, attracting fish by light, odors, sounds, and objects (Ben-Yami 1976, Bardach et al. 1980, Johannes 1981; see Parrish 1999 this issue). Fishing exerts selective pressures on a variety of behavioral phenotypes that may affect population viability. Impacts can potentially be felt even when non-reproducing animals are involved, particularly for those animals that play a role either in the cultural transmission of behavior or in parental care. Fishing pressure can also cause ripple effects on community structure (Persson et al. 1997). We need to have a much better understanding of the behavioral consequences of intensive fishing pressure so that we can make appropriate recommendations for single- and multi-species fisheries management plans.

The social organization of fishes, like that of other vertebrates, is affected by three different parameters: ecological, demographic, and the social activities of interacting conspecifics (Lott 1991). Changes in group size due to human exploitation can affect any or all of these parameters, and as a result, change social structure. The effects of human exploitation may be most damaging for the mobile, closed, and hierarchically structured groups found in elephants, pronghorns, and wolves (Lott 1991, Prins et al. 1994, Haber 1996). While the social structure of fishes has not yet shown to be as complex (Sale 1978), kin recognition has been shown in salmon and trout (cited in Brown & Brown 1993) and changes in social organization have been observed as a result of fishing. Studies on the effect of increasing fishing pressure on the bluegill, *Lepomis marcrochirus*, showed corresponding increases in the

proportion of individuals utilizing the alternative reproductive style of cuckolding (Drake et al. 1997).

Fisheries often select fish based on body size (Munro 1983). Selectively fishing large individuals may lead to a loss of experienced fish that provide cultural transmission of such factors as migration, food acquisition paths, and fear of predators. In bluegill, intensive fishing led to selection favoring parental males that were younger and smaller size at maturity (Drake et al. 1997). The consequences for parental behavior are unknown. Dugatkin & Godin (1993) showed that age affects imitative behavior in the guppy, *Poecilia reticulata*: young females copied the mate choice of older conspecifics, but not vice versa.

Selectively fishing large individuals can bias sex ratios in sequentially hermaphroditic fishes, such as groupers, labrids, and scarids which can affect reproductive success. The effect of fishing on sex ratios will be most damaging for those species where sex change occurs by endogenous control, dependent on age or size (Russ 1991). Overfishing aggregate spawners can also lead to marked skewing of sex ratios and population declines (Coleman et al. 1996, see Beets & Friedlander 1999 this issue).

Intensive fishing can affect other behavior. Schools are often selectively fished because of ease of capture. Twelve of the world's 20 most heavily fished stocks are schooling species (see Parrish 1999 this issue). Overfishing can affect school size, which can have a profound effect on the behavior of the remaining individuals, such as reduced time spent foraging, reduced efficiency in foraging, and increased timidity (Magurran & Pitcher 1983, Baird et al. 1991). Pitcher & Parrish (1993) cited a study by Itazawa et al. (1978) showing that fish in smaller groups have higher respiratory rates and are more nervous. Minnows actively chose a larger shoal size in a predatory environment (Hager & Helfman 1991).

Fishing pressure can also lead to shifts in habitat selection, as documented by Johannes (1981) for the large scarid, *Bolbometopon muricatum*. These parrotfish moved their sleeping sites to the deeper reef slope because of intensive spearfishing at their shallower sleeping site.

Exotic species.– Exotic species are a particular threat to endemic species already stressed by other anthropogenic causes. Perhaps conditioning could be helpful in encouraging exotic predators to reduce consumption of a particular threatened prey. One could take advantage of the well-known taste aversion response to a

food stimulus that elicits illness, as has been applied in reducing coyote consumption of sheep and crow consumption of quail eggs (Gustavson et al. 1974, Avery & Decker 1994). Taste aversion can be elicited by a single exposure (i.e., one trial learning), and can last a lifetime (reviewed by Hall 1994). Even if the aversion is not permanent, it may temporarily reduce predation pressure on a threatened species.

Although I am unaware of studies that document one-trial taste aversion in fishes, one-trial learning in fishes has been demonstrated (Brown 1937, Beukema 1970, Riege & Cherkin 1971). Chemical feeding deterrents also exist, as demonstrated by fish aversion to certain seaweeds and to chemicals derived from seaweeds (Hay 1991), and shark aversion to the ichthyotoxin pardaxin emitted by the Red Sea Moses sole, *Pardachirus mormoratus*. Groupers, jacks, and surgeonfish have been similarly repelled by the intact sole (Clark 1974).

Another potential application could be the chemical conditioning of native fishes to develop a fright response to an exotic predator, which may reduce predator success. Chemically-mediated avoidance of predators can be culturally transmitted within and across certain fish species (Suboski et al. 1990, Mathis et al. 1996).

Actively reversing the decline of threatened, endangered, or overexploited wild populations

Reducing bycatch by improving the selectivity of fishing gear

The catching of unwanted fish has two direct consequences: it creates tremendous waste and it leads to a reduction of future catches of desirable large animals due to the deaths of smaller ones (Kenney et al. 1991). The science of bycatch reduction has been largely directed toward improving the selectivity of trawls (Wardle 1991, 1993). Separator trawls, square-mesh cod ends, roped cod ends, radial escape sections, and skylight trawls are methods currently used to provide escape 'holes' for certain sizes of fish and species (Averill 1991).

Species can be separated according to their initial response to a trawl mouth, their position within the net, and their differential response to a variety of sensory cues (visual, rheotactic, or both). Fish first detect the noise of the ship and trawl, but at close range the visual system predominates. Many, but not all, species exhibit an optomotor response, i.e., following a moving object with one's eyes and head to keep a stable image on the retina. Schooling fish usually show such a response, with the whole body moving with the moving trawl. As the mouth of the trawl surrounds the fish, the fish swim forward, just matching the towing speed of the gear. Depending on fish size and trawl speed, a fish can stay in this position for long periods until it becomes exhausted. Fish are captured by the trawl when they cannot maintain swimming speeds equal to trawl speed (Watson et al. 1992).

Species and size groups differ in their behavioral reactions to a trawl. These behavioral reactions can be manipulated, thereby reducing indiscriminate capture. Haddock and cod can be separated by position, using a net with a separation panel: cod stay close to the sea bed, whereas haddock rise to the top part of the trawl mouth (Wardle 1991). Shrimp can be separated from juvenile fish by taking advantage of the shrimps' backward escape response and the behavioral reactions of fishes to changes in water flow characteristics within the trawl (Watson & Taylor 1991). Juvenile fish that do not exhibit an optomotor response can exit a modified trawl through escape openings (Watson et al. 1992). Using black netting in the middle of the white trawl net elicits an aversive response, increasing escape ahead of this section (Glass & Wardle 1995, Glass et al. 1995). This type of netting has now been written into fishing regulations for parts of the Scottish North Sea (C. Glass personal communication). Species-specific responses to different light intensities and wavelengths have also been exploited to reduce the catch of nontarget species in net fisheries (Clark et al. 1986).

Additional research is needed to determine how to reduce damage to those fishes that escape from a fishing device. In the case of trawls, most escapes occur in the cod end. The survival of the fishes that escape, however, is doubtful because the fishes are acutely stressed in their crowded environment and their scales and fins are often damaged. If fishes were separated in the mouth of the trawl, injury would be less likely. If stimuli can be applied that override the optomotor response, the fishes could potentially escape the net. Such stimuli include crowding within the trawl, slowing trawl speed prior to haulback, trawl haulback, and the change in ambient pressure that occurs as the trawl is hauled up to the boat (Watson et al. 1992). Alternatively, stimuli that selectively frighten certain species may stimulate escape-burst swimming, which can be faster than the speed of the trawl. A diver swimming alongside a net and attempting to grab a fish elicited such escape-burst swimming (Wardle 1991).

A promising future manipulation involves the creation of virtual, or apparent, borders, which are borders without solid demarcation. A virtual border associated with a bottom trawl has two advantages: it minimizes damage to seafloor habitats and it causes no damage to escaping fishes. Bubble curtains have been used in set-net fisheries to herd fishes toward the net (Stewart 1981, Arimoto et al. 1993), and could potentially be adapted as a virtual border in trawl fishing, although not without concerted effort. Such an approach has been unsuccessful to date, due to problems of generating bubbles at depth and of forming a seemingly solid curtain of bubbles at higher trawl speeds. Light has also been used as a virtual border, enabling a trawl to operate off the seafloor (C. Glass personal communication).

Augmenting reproduction

The strongest application of behavior to augmenting reproduction has been in bird conservation (Curio 1996). Acoustic playback has been successfully used to attract seabirds to historic and new breeding grounds (Baptista & Gaunt 1997). This approach may be relevant for fishes that use acoustic communication in courtship and mating; some fishes have been attracted to species-specific calls and other acoustic stimuli (Myrberg et al. 1986, Popper & Fay 1993, Lobel & Mann 1995).

Bird conservationists have also boosted the number of surviving young birds of a threatened species with some behavioral 'tricks' (Baptista & Gaunt 1997), and a similar approach might be applicable to fishes. In some fish species with paternal care, females prefer to spawn with males possessing eggs already in their nest (e.g., sand goby, *Pomatoschistus minutus*, Forsgren et al. 1996; three-spined stickleback, *Gasterosteus* sp., Goldschmidt et al. 1993). Adding eggs or egg dummies to the nest may therefore promote increased spawning.

Seeding empty but otherwise suitable habitats with a few individuals might increase local population size for those animals that select habitat based on the presence of conspecifics, although it is often difficult to transplant any but small juveniles (G. Helfman personal communication). For fishes using olfactory cues in habitat selection (Sweatman 1988), one may be able to enhance settling on empty or depauperate reefs or other habitats by exploiting such cues. Exploitation of olfactory cues is regularly utilized in hatchery/recovery programs for salmon (Quinn et al. 1989).

Manipulating social organization might increase the number of reproducing individuals. For example,

dominance hierarchies have been documented in numerous fish species in which dominant individuals breed and reproductive suppression occurs in all others (Sale 1978). One might be able to remove a dominant individual for a brief period to enable other individuals to breed. Such an approach has been tried on captive golden lion tamarins (Kleiman 1980). To my knowledge, this manipulation has not yet been applied to fishes, but experimental removal of dominant male fish does change the status of nonbreeding individuals (e.g., cichlids Fox et al. 1997, cyprinids Constanz 1975, labrids Godwin et al. 1996).

For fishes with variable social systems, reproduction might be facilitated by providing the specific environmental conditions that cause a shift to territoriality (reviewed in Lott 1991), such as increasing habitat availability for reef fishes with the aid of artificial reefs. According to Lott, females are more harassed in a dominance system than a territorial system, which may have implications for fecundity. Effects on fecundity have been directly demonstrated in antelope (Copeland 1980).

Assessing biodiversity

Modeling population viability and population dynamics

The diversity of social systems and the determinants of social structure need to be better integrated into models of population viability to facilitate more accurate estimations of the number of reproducing individuals. For fish, this may mean assessing the reproductive consequences of dominance hierarchies, breeder versus sneaker males, nonreproducing males, helpers, etc., depending on the species. Social systems have been taken into account in population viability analyses of threatened woodpeckers and gorillas (Heppell et al. 1994, Harcourt 1995). A similar analysis is needed for heavily exploited fish species.

We also need a better understanding of the environmental and social determinants causing changes in social behavior to predict when and where such changes might occur. The social structure of fishes can show profound intraspecific variation due to changes in habitat, availability of food resources, territories, and population density (Lott 1991, Shapiro 1991, Munthali 1996). Three different mating systems (monogamy, polygyny, and polyandry) could be generated in some damselfish species depending on the size of their resident coral head (Fricke 1977).

Censusing and monitoring populations

Intercepting an animal's communication signals can be a rapid and effective technique for censusing and monitoring populations. Automated acoustic monitoring of vocalizations has been tried on both whales and fishes. Acoustic tracking of whale vocalizations and dolphin echolocation signals generated more accurate population estimates than visual tracking, and tracking of dolphin echolocation signals was also more accurate in monitoring feeding behavior (Freitag & Tyack 1993, Bloom et al. 1995, Clark et al. 1996). Passive acoustic detection of courtship and monitoring sounds in the damselfish, *Dascyllus albisella*, provided the capacity to monitor reproductive activity over long periods and over wide spatial scales (Mann & Lobel 1995). The temporal pattern of sound production observed corroborated the known crepuscular peak of spawning in these fish.

Given the importance of chemical signals in the aquatic environment (Atema 1980, Hara 1993), chemical monitoring could be an option as well. In terrestrial environments, chemical attractants have been used by entomologists to assess insect species numbers (Rebelo & Garofalo 1991). In aquatic environments, either the use of chemical attractants or analysis of chemical traces in the water might be possible.

Captive breeding and reintroduction programs

Captive breeding and reintroduction techniques are increasingly popular in the recovery of endangered species, as reflected in U.S. species recovery plans (Tear et al. 1993). Behavioral understanding of such factors as mate choice, appropriate social structure, and environmental influences on mating is essential in identifying species that may benefit from such an approach and in achieving reproductive success within a captive population (Conway 1980, Snyder et al. 1996). While techniques are improving, numerous reintroduction programs have failed (Beck et al. 1994). Part of the problem is the behavioral deficiencies of released animals (Conway 1980, Snyder et al. 1996). Behavioral problems in reintroduction programs are thought to be greatest for species that learn much of their behavior, require parental care, experience heavy predation, or require contact with a wild individual or other environmental influences during critical learning periods (Snyder et al. 1996).

All but the simplest animals have to learn many of their survival skills, obtained by trial and error, observation, and through direct instructions from their parents, siblings, other conspecifics, and even other species. Animals may need to learn orientation; feeding (e.g., how and where to catch prey, which plant or animal species are poisonous and which are highly nutritive); places to rest and sleep; how to avoid predators, including humans; and relationships between and within species (Conway 1980, Tudge 1992). Animals may also have to learn particular traditions unique to their own area such as knowledge of local topography for foraging routes (Curio 1996).

Evidence from a variety of vertebrates suggests early experience affects the ability to perceive, discriminate, and prefer certain odors (Hudson & Altbäcker 1994, Ayabe-Kanamura et al. 1999). If early exposure is not provided in captive breeding and reintroduction programs, this could affect behavior ranging from foraging to habitat selection. In salmon, early exposure to odors from natal waters is essential in habitat imprinting (Hasler & Scholz 1983). Early exposure to conspecific odors is also important in population-specific recognition, the function of which is still unclear (Courtenay et al. 1997). Enhanced peripheral sensitivity to artificial stimuli can be induced only during this sensitive period (Nevitt et al. 1994).

Aquaculturists might be able to improve the survival of prey fishes upon release into the wild by exploiting the role of learning in predator avoidance (Suboski & Templeton 1989, Smith 1997). In the three-spined stickleback, Tulley & Huntingford (1987) showed the importance of parental influence on anti-predator behavior and the subtle interaction between the effects of experience and site of origin. Anti-predator responses were tested with isolated fish. Fish receiving normal paternal care showed much greater anti-predator responses upon first exposure to a pike, relative to orphans raised with their siblings, but only if their father came from a site experiencing heavy pike predation. Fish whose parents came from sites experiencing light predation showed no effect relative to the presence or absence of parental care.

Captive breeding programs often inadvertently alter the behavior of animals, starting with the decision of which animals to bring into captivity (see Rakes et al. 1999 this issue). Such behavioral changes may prevent a successful reintroduction. After several generations in captivity, the behavior of descendants may be altered through (1) human interference in normal patterns of mate selection (Kleiman 1980); (2) failure to provide conditions that allow expression of the

full behavioral repertoire used by wild conspecifics (Campbell 1980); (3) regular association with humans, which can affect defensive or flight behavior (Campbell 1980); (4) inappropriate social conditions; and (5) conscious or even unconscious selection by breeders for behavioral phenotypes considered desirable, such as tameness, tractability, and early reproduction. Irrespective of human selective pressures, some behavioral types do not reproduce well in captivity, and their genetic contribution to the population will be lost (Kleiman 1980).

Loss of appropriate behavior is of concern when hatchery-reared juvenile fish are released to boost threatened populations (Hindar et al. 1991). Hatchery programs *must* attempt to minimize phenotypic and genotypic change in both morphological and behavioral traits to ensure that such programs are contributing to species recovery, rather than exacerbating species loss (Meffe 1992, Flagg 1994, Gross 1995). Unfortunately, current hatchery practices often cause phenotypic changes in fish behavior that are detrimental to the long-term survival of hatchery-raised fish upon release (Ersbak & Haase 1983, Heggberget et al. 1993, Fleming 1994). The offspring of both hatchery-raised trout and hatchery/wild hybrids showed lower survival after just two generations of rearing in a hatchery (Reisenbichler & McIntyre 1977). Similarly, hatchery-raised male coho salmon were less aggressive than the wild type, and were 62% as successful in breeding; hatchery-raised females were less successful in acquiring and defending nests, and 82% as successful in breeding relative to the wild type (Fleming & Gross 1993). Part of the difference in breeding success appeared to be due to a reduction in sexual selection pressures that influence morphological characters important in breeding competition, such as changes in the hooked snout and its associated teeth used in fighting (Fleming & Gross 1994).

Behavioral deficiencies are also a concern for the accidental release of farmed fishes, given the possibility of hybridization between farmed and wild fishes (Hindar et al. 1991) Escaped farmed salmon showed less discrimination in mate choice than wild types, being eight times more likely to hybridize with brown trout, *Salmo trutta*, than wild females (Youngson et al. 1993).

Hybrids of rainbow trout, *Oncorhynchus mykiss*, created from a long-domesticated stock (over 20 years in captivity) and a wild female were significantly more willing to risk predation exposure than wild trout (Johnsson & Abrahams 1991). Wild strains of juvenile rainbow trout have to continuously weigh the benefits of foraging against the risk of predation. In contrast, hatchery-raised trout experience no predation and compete for food thrown at the surface. Cautious individuals are at a disadvantage. 'Selection for high growth rate by hatcheries may therefore select against predator avoidance' (Johnsson & Abrahams 1991, p. 243). The behavioral difference appears to be inherited (from the male) since both strains were raised in tanks under identical conditions.

Changing human behavior associated with resource exploitation

Ultimately, understanding human behavior is essential for changing patterns of resource exploitation and for fostering conservation, since human behavior is at the root of conservation problems. Analysis of behavioral tendencies in group decision-making has helped in understanding conservation policy failures (Yaffe 1997). Environmental educators, too, are benefiting from principles gleaned from social psychology and social marketing.

Contrary to popular belief and counter to most efforts at environmental education, just providing knowledge does not necessarily change people's behavior. Humans, like other animals, are flexible in some behavior, whereas other behavior is less tractable. If people know that a given behavior causes environmental damage, but engage in it anyway, other motivating factors are involved (Krumpe & Ham[3]). These factors can include attitudes, values, gender, social norms, skills, economics, time, options, greed, laws, habit, and beliefs (Byers 1996).

Three general types of beliefs have been identified: *behavioral beliefs* (why a person engages in a particular practice); *normative beliefs* (how social norms influence behavior, originating from peers, family, priests, local leaders, etc.); and *control beliefs* (how much a person thinks he/she has control over the practice) (Ajzen & Fishbein 1977, Fishbein et al. 1991, Krumpe & Ham 1997). Any or all of these beliefs can be targeted for change in an education campaign.

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[3] Krumpe, E.E. & S.H. Ham. 1997. How beliefs can be used in communication programs to affect local conservation practices. 1997 Annual Meeting Society for Conservation Biology: 135.
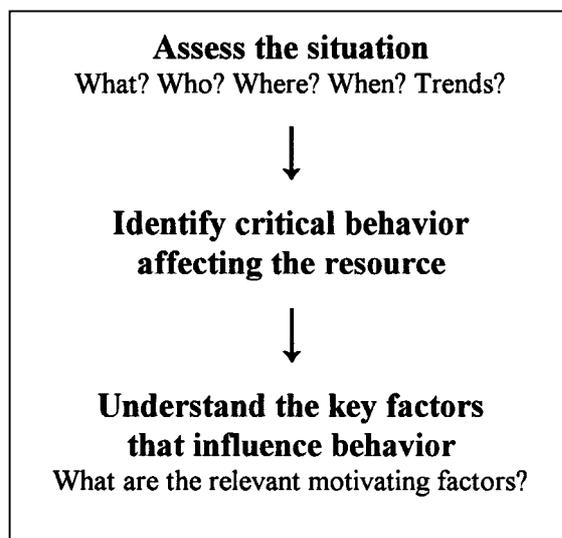
Assess the situation
What? Who? Where? When? Trends?

↓

**Identify critical behavior
affecting the resource**

↓

**Understand the key factors
that influence behavior**
What are the relevant motivating factors?

Figure 1. Steps in identifying the key human behavior responsible for a particular conservation problem (modified from Byers 1996, with permission).

In addition to environmental education, conservation projects can be more successful if practitioners incorporate the basic methods and tools of social assessment (Byers 1996). Social assessment at the beginning of a project can help identify those specific human actions that have the largest positive or negative impact on the environment or resource of interest, as well as identify the motivating factors that underlie such behavior (Figure 1). Behavior can then be ranked on the basis of feasibility of change. Such an approach is being tried by World Wildlife Fund with local communities surrounding Lake Nakuru National Park in Kenya (Byers 1996).

Conclusions

Behavioral science has much to contribute to conservation theory and practice. The examples presented here of links between fish behavior and conservation are just a beginning. The myriad ways behavior can contribute to the conservation biology of fishes is limited only by our imagination and inventiveness. How can we increase recognition of the valuable role behavior plays in conservation? First, we need a core and vocal constituency of behavioral scientists willing to get involved and to translate their work into useful and accessible conservation products (also see Pister 1999

this issue). Behavioral biologists studying fishes should highlight the applicability of their work to conservation and management in conferences, symposia, and journals devoted to conservation biology, along with the more specialized journals.

Second, we need to take advantage of the charismatic vertebrates in our midst: they are called fishes. The spectacular behavior of fishes is clearly an area of human fascination. People are often drawn to animals because of their unique or human-like behavior. The most popular exhibit at the London Zoo is not the terrestrial megavertebrates, but fishes (Balmford 1996). We should capitalize further on this public fascination with fishes and their behavior to advance our goal of conservation of the extraordinary wildlife found under water.

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