# **Response to Conditioned Stimuli by Two Rehabilitated and Released West Indian Manatees** (*Trichechus manatus latirostris*)

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#### Abstract

U.S. regulations discourage research that requires training with West Indian manatees (Trichechus manatus latirostris) due to the concern that trained manatees would become accustomed to approaching humans for food and would continue to approach people once released back to the wild. Learning theory suggests that behaviors acquired while in captivity may not transfer well to the new context of the wild habitat, however. In this study, two female, rehabilitating manatees were trained to perform up to five husbandry behaviors. Prior to their release, the behaviors were no longer reinforced. Response to training signals was reduced for all behaviors when reinforcement was withheld. In post-release observations, the manatees were located by satellite and radio-telemetry, and training signals were presented. Neither manatee performed any of the trained behaviors. The results of this case study suggest that training releasable manatees may be a viable option.

**Key Words:** West Indian manatee, *Trichechus manatus latirostris*, extinction, husbandry conditioning, research training, rehabilitation, reintroduction, context learning, endangered, Florida

#### Introduction

Oceanaria play a pivotal role in rehabilitating sick and injured manatees (*Trichechus manatus latirostris*) that have been rescued from the wild. The controlled environment of oceanaria offers unique opportunities for research with manatees that can contribute to the very limited knowledge base of manatee physiology and sensory systems. Reliable information about these systems could impact the management of this endangered species, a task that is becoming progressively more challenging as the coastal human population increases.

To gain knowledge that can contribute to management decisions, it is desirable to perform noninvasive studies that require behavioral training or conditioning. Additionally, both manatees and their handlers benefit from conditioning the manatees to participate voluntarily in veterinary procedures (see Colbert et al., 2001, for a discussion of the benefits). However, training animals that are destined to be released into the wild generates concern that these animals may become accustomed to accepting food and attention from humans and therefore be likely to seek out human interaction in the wild.

Because of this concern, the U.S. Fish and Wildlife Service (USFWS) has only permitted a small number of studies involving trained responses from manatees (e.g., Gerstein, 1994; Gerstein et al., 1999; Colbert et al., 2001; Bauer et al., 2003). Currently, there are only 14 manatees available for training and research: four are not under the jurisdiction of USFWS and cannot be considered for release, and ten have been deemed temporarily nonreleasable (N. Adimey, USFWS, pers. comm., October 2003). Although the status of these ten animals is temporarily nonreleaseable, medical conditions and management practices can and often do change. Thus, the possibility exists for each of these animals to be released to the wild at some point in the future.

In addition to the 14 manatees that are entrusted to long-term human care, there is an additional captive population of relatively short-term (i.e., a few days to more than 10 y), rehabilitating manatees that are recovering from illness or injury, were captive-born, or were orphaned. In many cases, manatees remain in human care for an amount of time that would be sufficient to conduct research.

Although training would be beneficial, the concern that it would lead to an increased propensity to interact with humans once released, despite the absence of experimental evidence, is pervasive. Even so, a substantial amount of evidence from laboratory work on learning theory leads to the prediction that trained responses would not be likely to be performed in the wild because, typically, there is only a weak transfer of learned behavior from one context to another (Domjan, 1998; Bauer, 2005; also see Gordon & Klein, 1994, for a review), and thus, a stimulus that elicits a conditioned response in captivity is less likely to elicit a response once the animal is returned to its natural environment (see Bauer, 2005, for a thorough discussion on this topic).

In addition to the effects of context change, one can further reduce the expression of conditioned behaviors through "extinction." Extinction is a fundamental process of learning observed in a wide range of species, including rats (Rattus norvegicus) (Nakajima et al., 2000; Denniston et al., 2003), horses (Equus caballus) (McCall & Burgin, 2002), toads (Bufo arenarum) (Muzio et al., 1992), turtles (Geoclemys reevesii) (Ishida & Papini, 1997), octopodes (Octopus digueti) (Michels et al., 1987), snails (Lymnaea sp.) (McComb et al., 2002), tarantulas (Aphonopelma hentzi) (Punzo, 2002), and honeybees (Apis mellifera) (Shinoda & Bitterman, 1987). Extinction can be defined as a reduced response to a conditioned stimulus because the response is no longer reinforced (Domjan, 1998). Specifically, the animal learns that performing the behavior no longer leads to the conditioned reinforcement (Domjan, 1998; Bouton, 2002).

Although extinction of learned behaviors occurs reliably in the absence of reinforcement, it should be noted that extinguished behaviors are subject to "spontaneous recovery" and can reemerge temporarily due to the passage of time or a change in context (Domjan, 1998). The effect of spontaneous recovery on the extinguished behavior is usually small, and the extinguished behavior normally disappears quickly after only a few unreinforced repetitions.

#### Training Releasable Animals

The behavior of released animals is important to conservation efforts (McLean, 1997), and many reintroduction programs incorporate training into their release procedures (e.g., Kleiman, 1989, 1996; Box, 1991; Treves & Naughton-Treves, 1997; van Heezik et al., 1999; Griffin et al., 2000; McLean et al., 2000; Brown & Day, 2002; see also Beck et al., 1994, for a review). Training regimes typically involve exposing potential releasees to conditions they will encounter in the wild such as naturalistic habitat, local prey, and live or model predators. Although at first glance the success of these programs may appear to contradict the predictions of the learning theorists, there are some important distinctions between typical pre-release training programs and the current study. Primarily, in pre-release training as well as in "soft release" programs, the goal is to reduce the differences between pre- and post-release contexts so that learned behaviors will be more likely to transfer to the wild setting. Secondly, success generally is measured by either assessing pre-release pro-survival behaviors, such as increased foraging or vigilance, or by measuring post-release survival rates. The likelihood of the animal performing specific, operantly conditioned behaviors that were learned in a captive setting has not been evaluated.

There are very few reports in the literature in which operantly conditioned animals have been released back to the wild, and none that assess retention of trained behaviors directly. Two attempts to release previously trained bottlenose dolphins (Tursiops truncatus) returned mixed overall results, although in neither case did the animals respond to previously trained stimuli. In one case (Wells et al., 1998), two subadult male dolphins were collected, maintained in captivity for behavioral research for two years, and then returned to their original home range. The dolphins were reacclimated to wild conditions by being maintained in a sea pen for one month prior to release, but there was no attempt reported to either extinguish or retain trained behaviors. In more than two years of follow-up observations, the dolphins were observed to be in excellent body condition and did not display inappropriate behaviors toward humans such as approaching or biting.

In a second case (Gales & Waples, 1993), nine Indian Ocean bottlenose dolphins were returned to the wild after the marine park in which they had been living closed. Five of the dolphins had been wild-caught from local waters 11 y previously. The remainder of the group comprised three juveniles and one newborn calf that had been born in captivity. The dolphins were reacclimated to wild conditions by residing in a sea pen for 3.5 mo prior to release. In contrast to the Wells et al. (1998) project, several recall and boat-following behaviors were intentionally trained or maintained in the sea pen in the hopes they would be retained post-release. Although all behaviors were trained in the sea pen, none were expressed after the dolphins were released. After release, all dolphins were observed to lose significant amounts of weight; three were returned to captivity, and the remaining six were not sighted again after periods ranging from 6 to 36 d.

It is difficult to assess the effects that operant conditioning had on these two groups of dolphins. Since both were trained but had drastically different outcomes, other factors, such as length of time in captivity, may have been more important to their success in the wild.

#### Goals of the Current Study

The purpose of this study was to test how two manatees would respond to conditioned stimuli once released back into their natural habitat. Prior to release to the wild, the trained behaviors were no longer reinforced (i.e., extinguished), and the decline of the behaviors was documented. After release, three follow-up field observations per animal were conducted in the manatees' natural environment. The trainers presented conditioned stimuli to determine whether the manatees would respond.

#### **Materials and Methods**

#### Subjects

Two female Florida manatees (Trichechus manatus latirostris), "Pine" and "Forest," were rescued together from Jacksonville, Florida, USA (30° 33' 46" N, 81° 65' 77" W), suffering from hypothermia. Both were transported to SeaWorld of Orlando, Florida, for 7 mo of acute rehabilitation and then transferred to The Living Seas, Epcot®, Walt Disney World® Resort, Lake Buena Vista, Florida, in July 2002, for follow-up care and to await the proper environmental conditions for release. The manatees' ages were estimated to be between 4 and 6 y based on their weights (372 kg and 454 kg, respectively) and lengths (228 cm and 232 cm, respectively). Their primary captive diet consisted of romaine lettuce with a supplemental diet composed of various fruits and vegetables, which were fed exclusively as training incentives ("primary reinforcement"). Also during training sessions, a dog whistle was conditioned as a secondary reinforcer to reward properly executed behaviors. The animals were housed with a variety of fish species in a public display pool (14.17 m x 7.16 m x 3.27 m), with an adjoining off-display medical pool (8.23 m x 4.42 m x 3.70 m). The dual, interlocking pool system contained 465,605 l of salt water.

### Initial Training

Training sessions occurred three times per day, five days per week. A primary trainer was assigned to each manatee to monitor the animal's progression through the successive stages of training, and each manatee was trained using standard operant conditioning techniques. Both animals were trained to perform four behaviors: (1) start-session, (2) target, (3) follow-target, and (4) ventral-present. In addition, Pine was trained to allow her pectoral flipper to be manipulated as if for a blood draw (Table 1). Ventral-present and manipulate-for-blood were designated as advanced behaviors because they required that a basic behavior be performed immediately before one could ask for them (i.e., the manatee could not be asked for a ventral-present if it had not targeted into the proper position relative to the trainer first). There was an imposed time

limit of 7 min for the manatee to come to station for the start-session behavior to be considered a success. Even considering the travel distance from the medical pool and the slow-moving nature of manatees, the training staff determined this to be more than sufficient time to respond. The manatees had up to 30 sec to respond to all other signals; however, at the trainer's discretion, she or he could elect to repeat the same signal within the 30-sec time period. If the behavior was not performed to criteria within 30 sec of the first signal, the manatee was scored as not responding. It should be noted that such unusually large response latency tolerances were deliberately chosen so that it would be possible to score the manatees as responding to a signal even though their response latencies may have been longer than normal once released to the wild environment. During training, the manatees typically arrived at their stations in response to the start-session signal within 3 to 5 min and responded to all other signals within 2 to 7 sec. Initially, reinforcement was provided on a continuous reinforcement schedule. In later stages of training, trainers could institute an intermittent reinforcement schedule at their discretion.

The husbandry behaviors were trained and maintained by the primary and other trainers over a period of 5 mo. Originally, the release date was scheduled for early March; however, due to weather conditions necessitating an earlier release, the manatees were exposed to approximately only 2 wks of extinction for advanced behaviors (while basic behaviors were still reinforced) and then 3 wks of extinction of both basic and advanced behaviors until their release on 18 February 2003 (Table 2). During extinction trials, the trainer presented signals as normal. If the manatee responded to the signal by performing the behavior, the trainer did not reinforce the behavior with either a primary or secondary reinforcer (i.e., food or whistle) and then allowed the manatee to selfterminate the behavior. Trainers presented signals ad libitum as long as the manatees were present at station.

#### Documenting the Frequency of Conditioned Response: Baseline Versus Extinction

Data collection began when, in the opinion of each manatee's primary trainer, the required behaviors had been learned. A continuous sampling method (Martin & Bateson, 1993) was used with each animal to document the true frequency of all stimuli given by the trainer and whether the manatee responded correctly. Trainers presented signals at their discretion and reported whether the manatee performed the behavior. One observer per trainer/ manatee pair recorded each signal and response. The response latency from when the signal was

Behavior	Signal	Criteria
Start-session	Splashing, slapping the water, or snapping fingers underwater <sup>1</sup>	Approach and stationing within 1 m while oriented toward the trainer within 7 min of first signal
Target	Palm of open hand or a target pole	Approach within 5 cm of target
Follow-target	Moving target	Remain within 8 cm of target
Ventral-present	Two to three taps by trainer's finger on man- atee's shoulder, 5 cm dorsal to the pectoral flipper pit	Roll onto dorsal side, exposing ventrum, and holding for a minimum of 2 sec (i.e., not a barrel roll)
Manipulate-for-blood	Massage, rub, bend, or apply firm, digital pressure on pectoral flipper as if preparing for a blood draw	Allow manipulation for a minimum of 10 sec and until released by the trainer

Table 1. Signals and criteria for a successful response by a manatee for each behavior trained

<sup>1</sup> For the start-session signal, the signal was given once and then given again if necessary after 1 min had elapsed and the manatee still had not arrived at station. The trainer could then continue to signal at his or her discretion for up to 6 min. All splashes, slaps, and snaps given within the 7-min time period were considered to be a single start-session signal.

given until the manatee arrived at station was recorded for the start-session behavior. When the behavior was not performed, latency was recorded as the maximum time allowed for the behavior (i.e., 7 min). The frequency of response to each stimulus for the initial 20 trials of the data collection period (while reinforcement was still being provided) was used as a baseline measurement of trained response. Performance during baseline measurements was compared to the last 20 extinction trials of each behavior before the manatees' release.

#### Post-Release Observation of Response to Training Stimuli

When environmental conditions were favorable for the manatees' reintroduction to the wild, a satellitetag was attached to each animal using protocols outlined by Deutsch et al. (1998) and released into the warm water source of Blue Spring, adjacent to the St. John's River, Florida, USA (28° 56' 53" N, 81° 20' 25" W). A total of three follow-up field observations per animal was conducted approximately monthly post-release; one or two sessions were conducted during each visit. A boat was used to locate each animal using satellite- and radiotelemetry. Once the animal was sighted, a floating swim platform (1.5 m x 2.3 m, Model PPK1002, Connect-A-Dock, Adair, IA USA) was launched from the boat and used as the stage for observations and presenting conditioned stimuli. The platform was paddled to within 10 m of the manatee using canoe paddles and then secured with an anchor. The anchor was lowered quietly into the water until it came to rest on the muddy bottom so as not to startle the manatees. On one occasion with Pine, high winds and a strong countercurrent prevented a close approach to the manatee, and the session was started at a distance of 50 m. Test sessions were initiated by one of the primary trainers using the same 7-min start-session signal as was conditioned while the manatees were in captivity.

Table 2. A timeline of events; the release date is represented as Week 0.

Date	Weeks	Event	
11 January 2002	-57.5	Both animals rescued due to hypothermia	
29 July 2002	-29.0	Transferred to the Living Seas and training initiated	
03 January 2003	-6.5	Began baseline data collection of trained behaviors	
14 January 2003	-5.0	Began extinction of advanced behaviors	
27 January 2003	-3.0	Began extinction of basic behaviors	
18 February 2003	0.0	Release date	
11 March 2003	3.0	1st post-release follow-up (both animals)	
16 April 2003	8.0	2nd post-release follow-up (Forest)	
25 April 2003	9.0	2nd post-release follow-up (Pine)	
19 May 2003	13.0	3rd post-release follow-up (Pine)	
25 June 2003	18.0	3rd post-release follow-up (Forest)	
25 June 2003	18.0	Final confirmed sighting of Forest	
22 January 2004	48.0	Final confirmed sighting of Pine	



Figure 1. A manatee in the ventral-present position; the rightmost trainer is holding the manatee's pectoral flipper as the leftmost trainer prepares to deliver food to the manatee's mouth.

Signals for other behaviors were presented opportunistically. Responses were documented using the same continuous sampling method described above. Video documentation also was used.

#### Results

## Pre-Release Response to Training Stimuli

The frequency of response during the last 20 extinction trials before release as compared to the first 20 baseline trials was reduced for both animals on all behaviors (Figure 2). Responses generally began to decline within the first or second session in which they were no longer reinforced, and performance between basic and advanced behaviors diverged when they were reinforced differentially (Figure 3). For Pine, the average response latency to the start-session signal increased from an average of 3.11 min (n = 20 sessions, SE = 0.69) during baseline training trials to 6.34 min (n= 20 sessions, SE = 0.46) during extinction trials. For Forest, latency increased from an average of 4.76 min (n = 20 sessions, SE = 0.61) to 5.70 min (n = 18 sessions, SE = 0.60; latency was not recorded in two of the final sessions for Forest due to observer error).

# Post-Release Behavior and Response to Conditioned Stimuli

Upon initial sighting during follow-up field observations, Pine was accompanied by conspecifics and was feeding on two of three occasions. Forest was observed with conspecifics and was feeding on all three sightings. Weather conditions were poor during the second follow-up with Pine. She was discovered resting alone in a sheltered cove and remained stationary throughout the observation—behavior that is typical of manatees in the St. John's River during inclement weather (M. Ross, Wildlife Trust, pers. comm., 25 April 2003).

On five of six occasions, the animals displayed interest in and began to approach the floating platform (previously a novel stimulus) when it was launched and paddled toward them. In four of five observations in which there was initial interest in the platform, once the paddling stopped and the platform was quietly secured, the manatee either stopped moving or changed heading, appearing to avoid the platform. The only exception was the first follow-up observation with Pine in which she circled the platform at a distance of 1 to 15 m for approximately 40 min.

The start-session signal was presented to Pine a total of four times and to Forest a total of six times. Neither manatee met the criteria for a successful start-session behavior; that is, neither oriented toward the trainer from a distance of 1 m within the 7-min time limit. Forest's zero of six responses were significantly fewer than would be expected by chance (binomial probability = 0.0156). For Pine, four signals were not sufficient to determine whether zero responses were statistically fewer than would be expected by chance. The loss of her telemetry tag prevented further follow-up.

In addition to the start-session signals, 13 target signals were presented to Pine during the first test session in the field. She maintained her proximity to the platform, but did not meet the criteria for a successful response to any signals. For the remainder of the test sessions, both manatees either did not respond or actively moved away from the start-session signals. In particular, on the final follow-up observation with Pine, the manatee came to a stop 9 m from the platform when the anchor was placed. The animal remained stationary and oriented toward the platform for 1 or 2 min until the trainer splashed the water as the first start-session signal, at which time she turned away and resumed feeding on natural vegetation.

#### Discussion

Both manatees responded to fewer conditioned stimuli during extinction trials than during the baseline training trials; however, without a control group, it is not possible to determine whether the reduction of responses was due primarily to the extinction procedure or to some other factor such as a seasonal disruption of behavior. Although other factors cannot be ruled-out, the 2-wk period of time during which reinforcement was withheld following only advanced behaviors, but not basic behaviors, can help separate the effect of extinction procedures from possible environmental or seasonal effects. The fact that the performance of the advanced behaviors declined when they were no longer reinforced, but that performance of basic behaviors generally was maintained during this period, suggests that manatees respond to extinction procedures in a way that is typical of other species.



**Figure 2.** Response to conditioned signals by two manatees under reinforcement vs extinction conditions; each stimulus was presented 20 times in each condition with the following exceptions: Manipulate-for-blood (Pine) was presented 9 times during extinction (with 4 responses), and follow-target (Forest) was presented 11 times during extinction (with 8 responses). Percentage of responses declined for each behavior.

The nonresponse of both manatees to all trained signals in the wild suggests that either the extinction procedures were effective, that the learning that took place while in rehabilitation did not transfer to the natural context, or that the manatees were not sufficiently motivated by the possibility of receiving food from humans. Of course, it is possible that a combination of these and/or other factors was important. The tendency of both manatees to approach the floating platform as it was paddled into position was an interesting, unanticipated behavior. Neither manatee had any prior experience with this platform while at the Living Seas; therefore, any attraction they had toward the platform cannot be explained by training or platform-food associations. Arguably, the attraction may have been directed toward the humans on the platform.



Figure 3. Response to conditioned signals per phase of extinction by two manatees; overall, performance was strongest during the baseline period in which all correct responses were reinforced. When basic behaviors, but not advanced behaviors, were reinforced, the response rate for basic behaviors remained generally high while the rate for advanced behaviors declined. Only signals for basic behaviors were presented in the field condition; neither animal responded to any of the signals given in the field.

Alternatively, the sound of water lapping against the side of the platform or the splashing of the canoe paddle used to propel the platform may have served as attractants, as attraction to novelty has been reported elsewhere (Gerstein, 1994). Once conditioned stimuli were presented (with the humans still present), including splashing the water, the attraction waned, however, and the manatees did not continue to approach. If the manatees were indeed attracted to the humans, the attraction could be related not only to their training history but also could be the result of positive associations created during routine exposure to humans throughout the manatees' 13 months of rehabilitation. Further studies that include nontrained, rehabilitated and nonrehabilitated manatees could elucidate whether any underlying attraction to humans is related to formal training, to casual exposure to humans during routine care, or is an expression of natural curiosity.

Pine was last sighted in February 2004 near her release site. She was in excellent body condition and possibly pregnant. Due to the loss of her satellite tag and lack of distinctive markings, Forest was not sighted again after our final follow-up visit on 25 June 2003, approximately 95 km from her release site. The water was not clear enough to assess her body condition. Both animals were observed socializing regularly with other manatees on several occasions (M. Ross, Wildlife Trust, pers. comm., 8 July 2004).

A few notes about the training process are worth mentioning. Although the manatees were responsive to both training and extinction procedures, the process was not without some challenges. Responses to the husbandry signals were reduced when no longer reinforced but were not completely eliminated. We believe there may have been two reasons for this. First, behaviors were interdependent in that performance of a particular behavior (e.g., manipulate-for-blood) often required that precursor behaviors (e.g., start-session, target, and ventral-present) be performed first. This created a situation in which it was difficult to extinguish each behavior fully individually because, as the manatees began to refuse to respond to unreinforced signals for precursor behaviors, it became impossible to present signals for more advanced behaviors. The decision to extinguish advanced and basic behaviors in two phases was an effort to mitigate this effect and extinguish as many behaviors as possible. Future researchers and trainers may want to consider extinguishing a single behavior at a time so that complete extinction can be achieved for every behavior prior to release. Conversely, it may be more efficient to only extinguish a few "keystone" behaviors upon which other behaviors are dependent (Barnett et al., 1996).

The second hindrance to completely extinguishing all of the husbandry behaviors was the general variability in the manatees' willingness to participate in sessions. Inconsistent performance has been observed in training programs at other facilities and does not appear to be an unusual trait for manatees (D. Colbert, pers. comm., 3 September 2003). Not surprisingly, this trend of nonparticipation increased substantially once reinforcement was no longer provided. Colbert et al. (2001) hypothesized that because manatees are grazing animals and only receive a small portion of their daily ration of food during training sessions, stimulus control may be weaker than for other marine mammals that are predatory carnivores and receive most of their food during training sessions. This is true even when the type of food provided during training is preferred and not otherwise available outside of training sessions. Variable performance was particularly characteristic of Forest in both the training and extinction phases of the study. Whatever the cause, the reduced number of productive sessions resulted in fewer opportunities to present signals to the manatees and a longer-than-anticipated timeline for both training and extinction. Although extinction progressed generally as expected, 6 mo was not a sufficient period of time to meet all training and extinction goals.

Given our preliminary findings, training releasable manatees may well be a feasible solution to more effectively managing captive manatees through husbandry training, as well as to the severe shortage of trainable research subjects. Neither manatee responded to any trained signals once released back to the wild, even though both manatees responded at least occasionally to signals during extinction prior to release. This outcome is consistent with context-dependent learning in that behaviors that are learned in one context are not expressed readily in a different context.

To help protect this endangered species, more must be learned about its behavior, sensory systems, and cognition. Since all but four manatees currently in human care are potentially releasable, the only option for conducting behavioral studies in controlled settings is to use potentially releasable animals. The results of this case study demonstrate that training releasable manatees may be a viable course of action.

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#### Literature Cited

- Barnett, D. W., Bauer, A. M., Ehrhardt, K. E., Lentz, F. E., & Stollar, S. A. (1996). Keystone targets for change: Planning for widespread positive consequences. *School Psychology Quarterly*, 11(2), 95-117.
- Bauer, G. B. (2005). Research training for releasable animals. Conservation Biology, 19(6), 1779-1789.
- Bauer, G. B., Colbert, D. E., Gaspard, J. C., III, Littlefield, B., & Fellner, W. (2003). Underwater visual acuity of Florida manatees (*Trichechus manatus latirostris*). *International Journal of Comparative Psychology*, 16, 130-142.
- Beck, B. B., Rapaport, L. G., Stanley Price, M. R., & Wilson, A. C. (1994). Reintroduction of captive-born animals. In P. J. S. Olney, G. M. Mace, & A. T. C. Feistner (Eds.), *Creative conservation: Interactive management of wild and captive animals* (pp. 265-286). London: Chapman & Hall.
- Bouton, M. E. (2002). Context, ambiguity, and unlearning: Sources of relapse after behavioral extinction. *Biological Psychiatry*, 52, 976-986.
- Box, H. O. (1991). Training for life after release: Simian primates as examples. *Symposia of the Zoological Society of London*, 62, 111-123.
- Brown, C., & Day, R. L. (2002). The future of stock enhancements: Lessons for hatchery practice from conservation biology. *Fish and Fisheries*, 3, 79-94.
- Colbert, D. E., Fellner, W., Bauer, G. B., Manire, C. A., & Rhinehart, H. L. (2001). Husbandry and research training of two Florida manatees (*Trichechus manatus latirostris*). Aquatic Mammals, 27(1), 16-23.
- Denniston, J. C., Chang, R. C., & Miller, R. R. (2003). Massive extinction treatment attenuates the renewal effect. *Learning and Motivation*, 34(1), 68-86.
- Deutsch, C. J., Bonde, R. K., & Reid, J. P. (1998). Radiotracking manatees from land and space: Tag design, implementation and lessons learned from long-term

study. *Marine Technology Society Journal*, 32(1), 18-29.

- Domjan, M. (1998). The principles of learning and behaviorl (4th ed.). Pacific Grove, CA: Brooks/Cole. 435 pp.
- Gales, N., & Waples, K. (1993). The rehabilitation and release of bottlenose dolphins from Atlantis Marine Park, Western Australia. *Aquatic Mammals*, 19(2), 49-59.
- Gerstein, E. R. (1994). The manatee mind: Discrimination training for sensory perception testing of West Indian manatees (*Trichechus manatus*). Marine Mammals: Public Display and Research, 1, 10-21.
- Gerstein, E. L., Gerstein, L., Forsythe, S. E., & Blue, J. E. (1999). The underwater audiogram of the West Indian manatee (*Trichechus manatus*). Journal of the Acoustical Society of America, 105(6), 3575-3583.
- Gordon, W. C., & Klein, R. L. (1994). Animal memory: The effects of context change on retention performance. In E. C. Carterette & M. P. Friedman (Series Eds.) & N. J. Mackintosh (Vol. Ed.), *Handbook of perception and cognition: Animal learning and cognition* (2nd ed.) (pp. 255-279). San Diego: Academic Press.
- Griffin, A. S., Blumstein, D. T., & Evans, C. S. (2000). Training captive-bred or translocated animals to avoid predators. *Conservation Biology*, 14(5), 1317-1326.
- Ishida, M., & Papini, M. R. (1997). Massed-trial overtraining effects on extinction and reversal performance in turtles (*Geoclemys reevesii*). *Quarterly Journal of Experimental Psychology, Section B*, 50B(1), 1-16.
- Kleiman, D. G. (1989). Reintroduction of captive mammals for conservation. *Bioscience*, 39, 152-161.
- Kleiman, D. G. (1996). Reintroduction programs. In D. G. Kleiman, M. Allen, K. Thompson, S. Lumpkin, & H. Harris (Eds.), Wild mammals in captivity: Principles and techniques (pp. 297-305). Chicago: University of Chicago Press.
- Martin, P., & Bateson, P. (1993). *Measuring behaviour: An introductory guide*. Cambridge: Cambridge University Press.
- McCall, C. A., & Burgin, S. E. (2002). Equine utilization of secondary reinforcement during response extinction and acquisition. *Applied Animal Behaviour Science*, 78(2-4), 253-262.
- McLean, I. G. (1997). Conservation and the ontogeny of behavior. In J. R. Clemmons & R. Buchholz (Eds.), *Behavioral approaches to conservation in the wild* (pp. 132-156). Cambridge: Cambridge University Press.
- McLean, I. G., Schmitt, N. T., Jarman, P. J., Duncan, C., & Wynne, C. D. L. (2000). Learning for life: Training marsupials to recognize introduced predators. *Behaviour*, *137*, 1361-1376.
- McComb, C., Snagha, S., Qadry, S., Yue, J., Scheibenstock, A., & Lukowiak, K. (2002). Context extinction and associative learning in Lymnaea. *Neurobiology of Learning* and Memory, 78(1), 23-34.
- Michels, J., Robertson, J. D., & Young, J. Z. (1987). Can conditioned aversive tactile stimuli affect extinction

of visual responses in octopus? Marine Behavioral Physiology, 13(1), 1-11.

- Muzio, R. N., Segura, E. T., & Papini, M. R. (1992). Effect of schedule and magnitude of reinforcement on instrumental learning in the toad, *Bufo arenarum. Learning* and Motivation, 23(4), 406-429.
- Nakajima, S., Tanaka, S., Urushihara, K., & Imada, H. (2000). Renewal of extinguished lever-press responses upon return to the training context. *Learning and Motivation*, 31(4), 416-431.
- Punzo, F. (2002). Reversal learning and complex maze learning in the spider Aphonopelma hentzi (Girard) (Araneae, Theraphosidae). Bulletin of the British Arachnological Society, 12(4), 153-158.
- Shinoda, A., & Bitterman, M. E. (1987). Analysis of the overlearning-extinction effect in honeybees. *Animal Learning and Behavior*, 15(1), 93-96.
- Treves, A., & Naughton-Treves, L. (1997). Case study of a chimpanzee recovered from poachers and temporarily released with wild conspecifics. *Primates*, 38(3), 315-324.
- van Heezik, Y., Seddon, P. J., & Maloney, R. F. (1999). Helping reintroduced houbara bustards avoid predation: Effective anti-predator training and the predictive value of pre-release behaviour. *Animal Conservation*, 2, 155-163.
- Wells, R. S., Bassos-Hull, K., & Norris, K. S. (1998). Experimental return to the wild of two bottlenose dolphins. *Marine Mammal Science*, 14(1), 51-71.