The Debate on Behavior in Conservation: New Zealand Integrates Theory with Practice

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Behavioral research is increasingly a part of species conservation, yet the debate over its relevance to conservation continues. We use New Zealand—a world leader in conservation management—as a case study to illustrate the integration of behavior and conservation. Advanced through adaptive management, conceptual behavioral research has been critical to the recovery of many threatened New Zealand species, and the percentage of published research addressing behavioral questions while being applied to conservation has grown considerably in the last 16 years. Much of this research has been incorporated directly into recovery plans for threatened species. Examples range from the cross-fostering of endangered native birds to behavioral plasticity of native fauna in the face of invasive rodents, to mating systems and potential control measures for invasive species. Our case studies not only address major themes in behavior but also provide reason for optimism about the future of the fledgling field of conservation behavior.

Keywords: animal behavior, conservation, management, threatened species, New Zealand

Behavioral research is increasingly a part of species conservation (Buchholz 2007), but debate over its relevance to conservation continues. In a recent commentary, Caro (2007) asserted that theoretical advances in animal behavior are unlikely to find utility in conservation, and he thus advocates a return to prosaic goals. Progress in science depends on integrating concepts into theoretical frameworks that provide testable hypotheses to guide scientific practice toward new knowledge and tools that in turn feed back into conceptual change (Peters 1991). Scientific maturation depends on progressing from description to evaluation and on to synthesis, and this maturation cannot occur in the absence of a theoretical framework (Altmann and Altmann 2003). Further, when two different fields merge, their integration is assisted and more successful if each discovers value in applying the different concepts, theoretical frameworks, and approach of the other.

There is a mismatch between conservation biology and behavioral research, but Linklater (2004) proposed a solution, termed "integrative pluralism," that applies a fundamental behavioral paradigm (Tinbergen's four questions; Tinbergen 1963) into conservation theory and practice to advance from parochially descriptive studies of behavior to behavioral problem solving. In this article we showcase advances and examples from New Zealand that illustrate the application of behavioral theory to species conservation. This approach gives reason for optimism, and we demonstrate progress in conservation behavior at both theoretic and pragmatic levels.

The New Zealand case study

There is no question that New Zealand ranks highly in its level of endemism, and that it has suffered major species declines and extinctions since human settlement and the arrival of invasive species (Gibbs 2006). New Zealand has no native terrestrial mammals, but it now supports a range of introduced mammals—one of the main causes of extinctions and continued threats to much of the endemic flora and fauna. For these reasons, New Zealand has a strong inherent commitment to conservation. For example, Bell (1991) reported that 39 percent of New Zealand contributions to an international ornithological congress were on conservation themes, compared with, on average, only 12 percent from other countries. This commitment to conservation-oriented research is apparent in New Zealand's governmental organizations (e.g., Department of Conservation, Landcare Research Limited) as well as in its universities. Indeed, many graduate research projects in ecology and biology are focused directly on nationally threatened species.

Because of the precarious status of much of its biodiversity, New Zealand has become a world leader in species management (Bell and Merton 2002). Rapid endangerment necessi-

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tated innovative and swift solutions that have been key to many successful recoveries. Advanced through adaptive management, behavioral research has been critical to the recovery of many threatened New Zealand species (Reed and Merton 1991). For 11 of 25 critically endangered bird species (44 percent), "behavioral techniques" are listed as a principle management tool (Bell and Merton 2002).

New Zealand conservation managers, unlike those in larger nations, appear to be less constrained by multilayered bureaucracy and conflicting interest groups when making decisions. Additionally, because the New Zealand conservation community is small and well connected, conservation-focused researchers usually communicate directly with easily accessible local managers, and thus research results can be quickly integrated into species recovery plans. Management decisions based on research results are often innovative and groundbreaking, albeit sometimes a balance of risks (e.g., the translocation of the endangered Hamilton's frog *Leiopelma hamiltoni* to Nukuwaiata Island from the small remnant population on Stephens Island; Tocher et al. 2006).

It is not surprising, therefore, that the conservation and behavior literature from New Zealand has grown dramatically during the last 16 years. Two searches of ISI's Web-of-Science bibliometric database (ISI Research Soft 2007), using "behavio* AND New Zealand" and "conservation AND New Zealand," with "New Zealand" also as an author's address search term, generated a similar number of behavior ($n = 657$) and conservation ($n = 647$) articles from 1991 to 2007 (articles from unrelated fields were removed). Annual numbers of behavior and conservation articles ranged from a low of 29 in the early 1990s to 138 in 2006, reflecting the growth observed globally in conservation and behavioral and animal biology generally (Linklater 2004). The sample of the conservation behavior literature and its authors was obtained from the intersection of the two searches (i.e., those articles and authors present in both the conservation and behavior literature). Fifty articles and their 40 leading authors were found in both searches. The contribution of conservation behaviorists has grown dramatically in recent years relative to the size of the behavioral literature (3 percent to 13 percent from 1991–2007).

Publishing patterns by conservation behaviorists in New Zealand indicate that their research addressed problems that were exclusive, as well as inclusive, of the other field (figure 1). The conservation behavior community in New Zealand, particularly among its most prolific publishers, is well represented by the two types of conservation behaviorists identified by Linklater (2004): (1) those whose main focus is conservation but who use behavioral research as part of larger multidisciplinary research objectives, and (2) those whose primary focus is animal behavior and who apply their expertise in conservation (figure 1). Overall, however, there were more conservation behaviorists whose publications span the conservation and behavioral literature equally. Thus, there is diversity in approach and perspective among conservation behaviorists, which explains why behavioral theory and practice has been so thoroughly integrated with

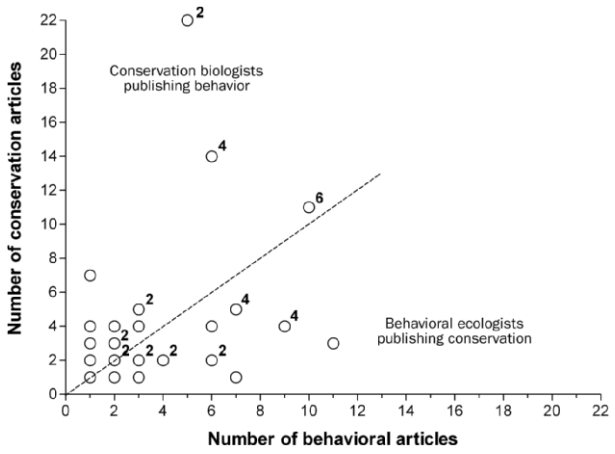

Figure 1. The relative contributions of the 40 leading authors whose 50 articles were featured in both the behavioral and conservation literature from New Zealand (1991–2007). The axes represent their total contribution to the behavioral (x-axis) and conservation (y-axis) literature. The community of conservation behaviorists is broadly based, from conservation biologists studying behavior in multidisciplinary research (upper left) to behaviorists applying their expertise to conservation (lower right). Numbers of articles that were present in both samples of the literature, and therefore classified as conservation behavior, are indicated by small numerals to the right of and above each open dot. Authors represented by dots without numbers published one conservation behavior article.

conservation in New Zealand, as we discuss in the next section. Nevertheless, the relatively low, but growing, proportion of articles that can be described as "conservation behavior" indicates that the potential for continued growth of the field is huge, such that the field might benefit from having its own specialist journals.

Integrative pluralism in conservation behavior

In his influential paper on ethology, Tinbergen (1963), noting that "ethologists differ widely in their opinion of what their science is about," proposed a paradigm uniting behavioral research through common themes, a paradigm that is still widely used today. Tinbergen's approach was advocated as a better way of understanding how behavior can be integrated with conservation (Linklater 2004, Buchholz 2007). The beauty of Tinbergen's four questions regarding causation, ontogeny, phylogeny, and adaptation is that they force us to consider multiple, complementary explanations for behavior, rendering ways of predicting and modifying behavior and behavioral outcomes in conservation. We adopt this approach here to demonstrate how fundamental questions in behavior have contributed to innovative conservation solutions in New Zealand.

Causative mechanisms. When applied to conservation questions, an understanding of behavior's causative mechanisms provides a route for understanding or manipulating behavior or allows us to predict the outcomes of ecological perturbations (e.g., climate change and exotic species invasion), or both. For example, Sol and colleagues (2002) analyzed factors affecting invasion success by 69 exotic bird species in New Zealand and Australia, and found relative brain size to be the strongest predictor. They concluded that behavioral flexibility (known to be correlated with brain size) is a major determinant of invasion success in birds. Theory on behavioral flexibility and brain size can be applied to explain and predict bird translocation success where limited behavioral repertoire or flexibility may have caused conservation efforts to fail. For example, many early attempts to translocate bellbirds (*Anthornis melanura*) were unsuccessful (Lee 2005). One of the reasons implicated in the failure is that naive birds were sourced from mammal-free islands and translocated to islands with mammalian predators, whereas birds could have been sourced from islands where they had been exposed to predators, as these birds were known to have modified their behavioral repertoire to coexist with predators (Lee 2005).

Rowe and Bell (2007) found that mate choice by reintroduced North Island kokako (*Callaeas cinerea wilsoni*) could be predicted from the similarity of the song repertoire of a chosen mate to that of kokako in the pretranslocation acoustic environment, a result that has direct application to future translocations of kokako and other rare birds. Trewenack and colleagues (2007) presented a model describing dispersal and settling of translocated animals and applied it to the translocation of the Maud Island frog (*Leiopelma pakeka*). The model showed that settling occurs at a constant rate, with repulsion (from chemical signals) probably playing a significant role. These examples demonstrate the utility of conspecific attraction or avoidance theory, which has been used in designing translocation programs for threatened seabirds (Gummer 2003, Stamps and Swaisgood 2006).

Sex allocation theory has played a role in conservation of one of the world's most endangered parrots, the kakapo (*Strigops habroptilus*). A strongly male-biased sex ratio of chicks jeopardized kakapo recovery until the cause of the bias was identified through sex allocation and parental investment theory, according to which mothers in good condition increase investment in male offspring (Clout et al. 2002). Excessive supplementary feeding, a common practice in species recovery programs, was replaced by a new optimized feeding regime through which the weight of all females rose just enough to boost breeding frequency while stabilizing the sex ratio of offspring; thus a major goal in kakapo recovery was achieved (Robertson et al. 2006).

Ontogeny. Behavioral learning and retention theory (e.g., operant conditioning) is finding growing application in conservation, particularly in predator-avoidance training of translocated wildlife, which improves postrelease survival rates. Exposing naive animals (which are often captive-reared or sequestered on islands) to artificial predators is designed to "teach" them to better evade real predators in the wild. McLean and colleagues (1999) presented young New Zealand robins (*Petroica australis*) with artificial predators, and demonstrated the ability of these naive birds to respond to the simulated predators with appropriate evasive behavior.

Another commonly used technique in avian conservation management is cross-fostering, whereby the young of a rare species are reared by surrogate parents in a closely related common species. Cross-fostering was successfully used for incubating eggs of the endangered takahe (*Porphyrio mantelli*) by a close common relative, the pukeko (*Porphyrio porphyrio*) (Bunin and Jamieson 1996a). The incubation of takahe eggs by pukeko was not only successful, but cross-fostered yearling takahe exhibited higher levels of alertness and avoidance than parent-reared takahe, indicating that cross-fostered animals can learn behaviors that will improve their success in the wild (Bunin and Jamieson 1996b). Cross-fostering has since been integrated into numerous species recovery plans, including takahe, fairy terns (*Sterna nereis davisae*), and black stilts (*Himantopus novaezelandiae*), or kakī, and is now widely implemented. Brood parasite and predator recognition theory has been key to understanding in which species, and under what circumstances, cross-fostering is most likely to succeed.

Theoretical and empirical knowledge of imprinting has minimized the problems associated with foster parents, including humans. Experience and an extensive literature on imprinting behavior of common and economically important species were critical to the success of conservation directives for threatened species in New Zealand. For example, takahe chicks have been routinely hand-fed using takahe-head puppets (figure 2) with internal speakers playing adult feeding calls (Eason and Williams 2001). Likewise, because young black robins (*Petroica traversi*) malimprinted on and hybridized with their Chatham Island tomtit (*Petroica macrocephala chathamensis*) foster parents, careful management was required, including translocation to a tomtit-free island (Butler and Merton 1992).

Adaptive value. Historically, the majority of studies involving a behavioral component in conservation address the adaptive value of the behavior (Linklater 2004). Knowledge of the adaptive value of behavior can be used to determine what impact an environmental change or conservation action might have on the performance (fitness) of individuals and populations through intended or unintended changes in behavior. The guiding theories in these studies focus on optimality (i.e., the expectation that fitness will be optimized or maximized). Examples range from monitoring the post-translocation behavior and success of birds (e.g., Armstrong et al. 1999) and investigating the effects of human presence on animal behavior (and, ultimately, fitness; e.g., Cole 1994), to understanding the behavior of introduced pests (e.g., Russell et al. 2005).

Figure 2. Captive raising endangered takahe chicks involves feeding with takahe-head puppets (left) and brooding under an adult female model (right), to avoid the chicks' imprinting on humans.

Ecotourism can adversely affect wildlife, and studying the behavioral responses of animals and their consequences for fitness is one way to gauge this form of human impact. In a study of the spatial patterns of fish in marine reserves, researchers found that large benthic fishes were attracted to divers—who often feed the fish—and thus the fishes' movement patterns are altered (Cole 1994). The attraction to divers and resultant changes in movement patterns confound attempts to assess the success of marine reserves at protecting fish from harvest, and very likely have adverse effects on large prey organisms. Human disturbance is also a problem on busy beaches, where seabirds and shorebirds nest. By approaching the nests of threatened New Zealand dotterels (*Charadrius obscurus aquilonius*), Lord and colleagues (2001) found that the birds were habituated to humans on busy beaches, and also that the biggest threat to normal avian parenting behavior came from dogs. The parent birds' avoidance behavior was strongest when they were approached by a dog, indicating that walking dogs near nesting seabirds may severely affect nest success. Because of the potentially devastating effects that dogs may have on bird survival, the New Zealand Department of Conservation has initiated an avian awareness and avoidance training program. Dog owners are educated about the dangers their dogs may pose to ground-dwelling native birds, and dogs are trained to avoid these birds.

Phenotypic plasticity theory can help predict and explain how native species interact with and respond to the threat of an exotic predator. For example, Hoare and colleagues (2007) found that large, nocturnal geckos (*Hoplodactylus duvaucelii*) were able to coexist with introduced and predatory ship rats (*Rattus exulans*) because they modified their movement patterns in the presence of rats. The authors concluded that the highly plastic spatial avoidance behavior of these geckos may enable short-term sympatry with introduced rats. Likewise, Rufaut and Gibbs (2003) reported that endemic tree weta (*Hemideina crassidens*) modified their behavior in the presence of introduced rats, suggesting that their behavioral flexibility may enable them to withstand a small degree of predation pressure from introduced vertebrates, which allows managers to prioritize conservation efforts.

Theory about the adaptive function of dispersal and its demographic implications is being applied to understand the behavior of invasive species. For instance, the dispersal behavior of Norway rats (Russell et al. 2005) is being used to predict invasion patterns and risk and to redesign biosecurity measures on island sanctuaries. Also, Stringer and Lester (2007), after investigating the mating system and foraging behavior of an invasive ant (*Monomorium sydneyense*), were able to predict that the potential ecosystem damage caused by this species would probably be very low compared with other invasive ant species.

Mating system theory has been used further to predict the applicability of biological control to invasive species. One of the greatest threats to New Zealand's biodiversity is an introduced Australian marsupial, the brushtail possum (*Trichosurus vulpecula*) (Jolly 1993). Biological control, in the form of a sexually transmitted immunocontraceptive, has been proposed as a potential control technique. To determine the potential efficacy of such a control, Sarre and colleagues (2000) investigated the mating system of possums and found that male reproductive success was extremely variable. The authors concluded that this highly polygynous mating system would very likely facilitate the spread of a sexually transmitted immunocontraceptive, which could be a potentially valuable possum control measure. Likewise, Ji and colleagues (2000) found that male possums were attracted to experimentally sterilized female possums, whose resultant prolonged period of estrus left males in poorer body condition and hence at greater risk of death. Their results bolster the viability of immunocontraception or sterilization as a method of control for this extremely destructive invader, and these options will most likely be employed in the near future.

Phylogeny. Studies of behavioral phylogeny and evolution, which have played a much smaller role in conservation (Linklater 2004) than the studies discussed above, may be an area in which behaviorists might expand their contribution. For instance, Paterson and colleagues (1995) found that a cladistic analysis of behavior reflected seabird phylogeny; the 18 species studied included albatrosses, petrels, and penguins. Their behavior and life-history data set (72 characters) was no more congruent than molecular data, and the resulting trees matched molecular trees. Again, Kennedy and colleagues (1996) revive the older ecological claim that behavioral characters could be used to provide accurate estimates of phylogeny, constructing a 37-character behavioral data set on the basis of van Tets' (1965) finding that parsimony analysis of 20 taxa produced 12 shortest trees that fit the behavior data well. Thus, we might consider that behavior should contribute to the definition of evolutionary significant units (or equivalent classifications) in conservation, particularly where behavioral theory predicts behaviors critical to fitness.

Life-history theory and the evolutionary transition from a recent *r*-selected colonizer to a *K*-selected endemic predict that many New Zealand avian species pairs are double invasions of the same stock (Fleming 1962; e.g., the *r*-selected pukeko, *Porphyrio porphyrio,* compared with the *K*-selected takahe, *Porphyrio mantelli*; Bell 1991). Differences between these two species include a suite of behavioral traits that explain the takahe's greater vulnerability to environmental disturbance and its current endangered status; therefore, its need for conservation management is greater than it is for its *r*-selected relative. Furthermore, in a test of the relative contributions of phylogeny and sociality to the evolution of play, Diamond and colleagues (2006) contrast the relatively solitary and highly endangered kakapo (*S. habroptilus*) with the more social kaka (*Nestor meridionalis*) and kea (*Nestor notabilis*). They concluded that social play in these parrots appears to be most readily predicted from their patterns of social development, emerging within a constellation of behaviors associated with independent young that remain in the vicinity of adult groups. Kaka and kea recovery plans now require captive-bred individuals to be raised in social groups, which aids normal development and improves the likelihood of success once the birds are introduced into the wild.

Conclusions

The examples we have highlighted, summarized in table 1, addressed fundamental behavioral questions and applied behavioral theory yet were integrated well into conservation to provide innovative solutions to problems. Although we offer numerous examples in which behavioral research was successfully applied to conservation, there have also been

Table 1. Summary of examples from New Zealand of successful integration of behavior to address conservation problems.

Behavioral question and examples	Reference(s)	Applicability to conservation
Causative mechanisms		
Relative brain size predicts invasion success in birds	Sol et al. 2002	Used to predict success/failure of bird translocations and aid in translocation programs
Kokako choose mates on the basis of song repertoire	Rowe and Bell 2007	Increased success of translocated kokako by matching the song repertoire of release cohorts
Chemical repulsion plays a role in settling of Maud Island frogs	Trewenack et al. 2007	Conspecific interactions integrated into designing translocation programs
Sex allocation theory invoked to explain male bias in kakapo chicks	Robertson et al. 2006	Kakapo supplementary feeding regime optimized, which increased reproductive output and equalized chick sex ratio
Ontogeny		
Predator training teaches young, naive birds to avoid predators	McLean et al. 1999	Increased success of translocated individuals that have learned to avoid predators
Cross-fostering increases hatching success and predator avoidance	Bunin and Jamieson 1996a, 1996b	Incorporated into recovery plans for numerous species, which has improved hatchling success, and translocated or captive-reared birds have learned predator avoidance
Adaptive/functional value		
Foraging and dispersal behavior of hihi not adversely affected by translocations	Armstrong et al. 1999	Immediate success of hihi translocations has been confirmed
Behavior of marine fish altered by human presence	Cole 1994	Altered protocols for determining success of protection from harvesting; modification of ecotourism management
Dogs elicit strong avoidance behavior of nesting shorebirds	Lord et al. 2001	Human presence on beaches with high shorebird nesting activity has been limited, avian awareness and avoidance training program initiated for dogs and their owners
Geckos modify spatial behavior in the presence of introduced rats	Hoare et al. 2007	Managers were able to prioritize costly pest eradication and predict effects on native species
Solitary introduced rats can disperse great distances (over water)	Russell et al. 2005	Increased biosecurity measures for invaders
Invasive ants (*Monomorium sydneyense*) are inefficient foragers	Stringer and Lester 2007	Potential biosecurity risks from these ants is very low, allowing managers to focus on more costly invaders
Invasive brushtail possums are highly polygynous; sterilizing females confers negative fitness consequences to males	Ji et al. 2000, Sarre et al. 2000	A sexually transmitted biological control measure may be highly effective
Phylogeny		
Cladistic analysis of behavior corresponds to molecular phylogenies of seabirds	Paterson et al. 1995, Kennedy et al. 1996	Aid in resolving evolutionary significant units or management units
Social play in parrots predicted from patterns of social development, not taxonomy	Diamond et al. 2006	Raising captive chicks in social groups is a compulsory part of the kea and kaka recovery plans, which improves the success of captive-bred birds in the wild
Life-history patterns explained for recent and early invasions of same stock	Fleming 1962, Bell 1991	Identifying behavioral tactics in *r*-selected common pukeko (recent colonizer) and *K*-selected endangered takahe (flightless endemic) help to explain the different conservation statuses of these species

early failures. We should now build on the recent successes that illustrate how we arrive at novel solutions when merging these two disciplines, and learn from failures that might have benefited from greater integration of behavior in conservation.

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