

Recognition behavior based problems in species conservation

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Recognition system theory was developed as a tool to investigate kin selection and mate choice, but can be applied to a wide variety of biological systems. Recognition behavior is central to species persistence, and might contribute to understanding and solving some problems in species conservation. In this paper I identify the role recognition behavior can play in some problems central to species conservation, including survey methods, habitat selection, mating success, maintaining genetic variability, predator avoidance, and pest deterrence and control. For each topic I identify ways in which taking advantage of the recognition template, threshold position, discrimination, or cue manipulation might be used to resolve species conservation problems. The framework that has been developed for studying recognition systems shows promise as a research framework for refining study of the behavioral issues affecting species persistence.

Introduction

Conservation biology as a scientific discipline is relatively new, and unlike most of the fields of study represented in this volume, it is an applied, multidisciplinary research field (Soulé 1986). Conservation biology has as its central goals identifying species, ecosystems, and ecological processes at risk of loss or endangerment, and identifying ways to reduce risks (Gilpin & Soulé 1986, Meffe *et al.* 1997). Practitioners are always looking for new tools for evaluating and reducing risk, and my goal in this paper is to provide a context for the application of recognition behavior to species conservation. I am focusing strictly on species conservation because recognition behavior is not applicable to ecosystems or ecological processes *per se*. This paper is part

of a growing effort to incorporate behavior into conservation biology. Even though behavior can have significant effects on species extinction risk and recovery (e.g., Reed 1999), the study and application of animal behavior outside of captive breeding (e.g., Gibbons *et al.* 1995) has had limited input in species conservation (Sutherland 1998a, Reed 2002). There has been some effort to ameliorate this, and to stimulate animal behavior research, through the publication of symposia specifically tying behavior and conservation (Clemmons & Buchholz 1997, Caro 1998, Gosling & Sutherland 2000, Festa-Bianchet & Apollonia 2003). Although these publications represent significant efforts in species conservation, it is too early to determine what impact they will have on the direction of research in animal behavior.

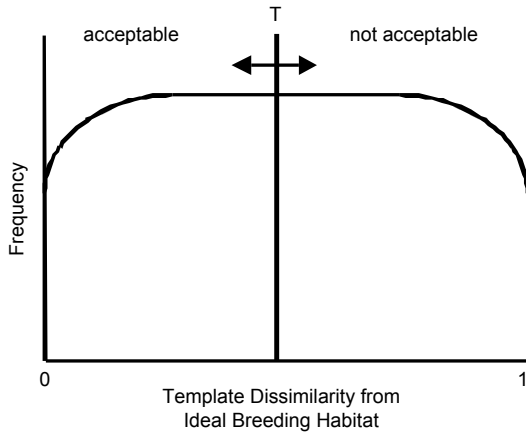


Fig. 1. Schematic of a recognition template for breeding site selection. The y axis refers to the frequency of individuals exhibiting cues with different dissimilarities. A deviation of 0 represents cues associated with the ideal breeding site, and the acceptance threshold (T) distinguishes the degree of deviation from the ideal at which habitat is no longer acceptable for breeding. Although the x-axis here and on the next figure are presented as a single axis, it should be acknowledged that this can be a multivariate variable, or that the template could be represented in multiple dimensions if there are multiple cues.

Recognition systems theory was designed initially as a tool to investigate kin selection, but can be applied to a wide variety of biological systems (Sherman *et al.* 1997, Starks 2004, and papers in this volume). The early development of recognition systems was done to provide a framework for quantifying decisions made by an individual evaluating cues associated with a conspecific. More recently, the study of recognition behavior broadened to incorporate any type of recognition and discrimination among cues, from an individual discriminating conspecific and heterospecific cues, or cues from inanimate objects (as might occur during habitat selection), to physiological processes such as the immune response (Sherman *et al.* 1997, Starks 2004, and papers in this volume). Here I focus mostly on individual behaviors, although there are physiological processes important to conservation biology that fit into a recognition system framework. Recognition system components include expression of cues (*see* Tsutsui 2004), perception and assessment of cues (*see* Mateo 2004), and actions taken after assessment (*see* Liebert &

Starks 2004). It is presumed that an individual's recognition system includes a template, or suite of templates, for decisions against which cues are compared. For each decision, the template includes an individual's ideal and the degree of acceptability as the cue or suite of cues deviate from the ideal. If an individual recognizes a cue, it can either accept or reject it; discrimination or action (which can include not altering behavior) is the behavioral outcome (Sherman *et al.* 1997). For example, an individual would have a template for the optimal habitat in which to place a breeding territory based on various cues associated with habitat quality, such as habitat structure, food availability, and presence of conspecifics. The individual then compares potential sites for territory placement and selects the available site that is closest to the ideal on its template (Fig. 1). Individuals are thought to have an acceptance threshold for each decision such that cues too dissimilar from the ideal on a template are rejected (Reeve 1989). Recognition behavior results in species characteristic preferences (e.g., Gravel *et al.* 2004), although there can be intraspecific variability, such as that caused by individual experiences (Sherman *et al.* 1997). There are two types of recognition errors an organism can make: reacting positively to a cue that is inappropriate, or rejecting a cue that is appropriate. An example of both recognition errors from conservation biology arose when eggs from the endangered whooping crane (*Grus americana*) were cross-fostered in sandhill crane (*G. canadensis*) nests in order to increase the number of whooping crane eggs incubated (whooping cranes lay 2 eggs, and one egg was removed from nests and cross-fostered to spread the risk of egg loss). Adult whooping cranes that came from eggs cross-fostered courted sandhill cranes rather than other whooping cranes (Mahan & Simmers 1992).

The recognition template and location of the acceptance threshold typically is not known *a priori*, but gathering sufficient information to determine the template form and threshold location can be important to species conservation. For example, recognition is used for habitat selection, and knowing the appropriate habitat cues is central to successful habitat restoration. Refining the cues, such as finding the best artificial nest

design and placement (e.g., Hirsh 1977, Copeyon *et al.* 1991), can be used to improve habitat restoration effectiveness. This has been done most extensively for hunted waterfowl, where habitat creation and restoration has been practiced for decades (if not centuries) with a goal of sustainable species harvest, which requires long-term species conservation (Payne 1992, Baldeassarre & Bolen 1994). Habitat design is both for features required for nesting (at breeding sites) and for food production. For example, ponds designed to attract blue-winged teal (*Anas discors*) for breeding are seasonal and shallow (13–20 cm deep water), with 50% vegetation cover, particularly sedges (*Carex* spp.), with the vegetation well interspersed with water, a diversity of macroinvertebrates, and adjacent upland grass or herbaceous cover for nesting (Fredrickson & Taylor 1982, Rohwer *et al.* 2002). This is achieved through a variety of techniques that can include vegetation burning, altering salinity, physical manipulation of the substrate, and water level manipulation for what is referred to as moist soil management, which uses water drawdown to produce appropriate plant and macroinvertebrate species (e.g., Fredrickson & Taylor 1982, Payne 1992). This type of detail in breeding site selection is not known for most species.

Consequences of discrimination and expected fitness costs of recognition errors also might be used to predict changes in mean population acceptance thresholds and the expected direction of evolutionary changes under a variety of conditions (Sherman *et al.* 1997). One possibility that apparently has not been considered in this type of analysis is the potential benefit of an acceptance error. Rare species sometimes hybridize with related species, which is a failure to reject an unsuitable mate. This is predicted by recognition system theory, whereby universal acceptance might occur when the expectation of finding a suitable mate is extremely low (Reeve 1989). However, this “error” can increase genetic variability in a relatively homozygous population, increasing mean fitness of a population (Rieseberg 1991, Grant & Grant 1992, Hedrick 1995). Grant and Grant (1992) found evidence of just over 9% of bird species hybridizing in the wild. In their detailed studies of Darwin’s finches (*Geospiza* spp.) they find that hybrids do not

have reduced reproductive success and they have higher survival rates. This combination results in higher fitness for hybrids.

Behavior has entered the field of conservation biology only through animal behavior, which affects plants or fungi only indirectly through processes such as pollination or propagule dispersal. However, recognition systems apply equally well to plants or fungi (e.g., Pfennig & Sherman 1995), so the possibility exists that a recognition behavior framework will broaden the contribution of behavior in species conservation, at least for evolutionarily based questions. Recognition behaviors are central to a wide variety of problems in conservation biology because they are fundamental to species existence and evolution through processes such as mate and habitat selection. There can be several measures of success in applying recognition behavior thinking to species conservation, including providing an organizing framework for identifying or discussing problems of species risk, allowing the prediction of species susceptibility to particular types of problems before they occur, allowing one to anticipate species responses to problems once they occur, and being used to identify solutions, or procedures for creating solutions, to species risks. My goal here is to identify the role recognition behavior has to some problems central to species conservation, including (1) survey methods, (2) habitat selection, (3) mating success, including maintaining genetic variability, (4) predator avoidance, and (5) pest deterrence and control. In each section, I will point out ways in which manipulating behavior, i.e., taking advantage of the recognition template, threshold, and discrimination might be used to solve species conservation problems. Because of space limitations I cannot cover all aspects of recognition behavior in conservation biology, and I will be able to cover only briefly each of the topics listed. However, my hope is that these brief reviews will stimulate subsequent research on recognition behavior and species conservation.

Survey methods

Determining the distribution, abundance, and population trends of species is a fundamental

problem in conservation biology (Orians 1997, Sutherland 1998b). Most species surveys are variations on the themes of detecting individuals using visual or aural cues (e.g., Bibby *et al.* 1992, Zimmerman 1994) or by capturing individuals or evidence of individuals (e.g., Cooperrider *et al.* 1986, Heyer *et al.* 1994). Both approaches are improved for some species by taking advantage of recognition behavior, using cues for food, mates, or competitors to increase detection probabilities. An excellent example comes from aural surveys of cryptic marsh birds such as rails (Rallidae) and bitterns (Ardeidae). These species tend to be behaviorally secretive, and although calls are important for intraspecific interactions, they do not occur at sufficient intervals to create reliable surveys (Conway & Gibbs 2001). However, these calls, which are used for territorial signaling and mate attraction, can be broadcast by a human surveyor and greater numbers of individuals can be detected. Conway and Gibbs (2001) reviewed data from published surveys of North American marsh bird, comparing estimates without and with call playback. They found that detection was increased for most rail species, including a 925% increase in detection probability for king rails (*Rallus elegans*), and that variance in detection in repeated surveys at a site was reduced. Using call playback is taking advantage of recognition behavior to achieve conservation goals: estimating population size, monitoring population trends, and gathering data on occupancy, which can be used to create habitat specificity models (Scott *et al.* 2002). Because playback is in its early stages of use, we do not know if there are biases in responses (e.g., between territorial and non-territorial males) that might affect population estimates.

One can take advantage of recognition behavior when using capture or capture-like survey methods as well. It is common to bait survey traps or detection stations for some species to act as an attractant to increase detectability (e.g., Call 1987, Powell *et al.* 1996). For example, in some species of salamander (e.g., spotted salamanders, *Ambystoma maculatum*) males can be surveyed during the breeding season using a minnow trap containing a female, which attracts males (Heyer *et al.* 1994). A physical model, or

decoy, might also be used to increase detection probabilities by attracting individuals to traps, as has been suggested for spotted turtles (*Clemmys guttata*) (Mansfield *et al.* 1998).

In each of these cases, survey methods were improved by understanding the recognition behaviors of targeted species. A great deal of effort is dedicated to improving survey estimates of population size and trend through development and refinements of statistical techniques. However, the limiting factor for effectiveness in all statistical techniques is species detectability (e.g., Buckland *et al.* 1993). Consequently, reducing detection error by refining survey techniques that take advantage of recognition behavior should be an effective line of research. For example, answering questions such as 'What is it that attracts male spotted salamanders to minnow traps containing a female?', 'Can it be isolated?', and 'Can it be improved upon, making a super-stimulus?', can take advantage of experimental protocols and might result in important conservation tools.

Habitat selection

Habitat selection involves processing and interpreting cues associated with expected fitness (e.g., Klopfer 1969, Fretwell 1972, Wiens 1989). Here I am referring to habitat selection on a fine scale, referring to selection of specific sites among alternative somewhat similar sites, rather than gross selection of, for example, forest over meadow. Habitat selection can occur for breeding, as well as during migration (seasonal two-way movements), foraging site selection, and non-breeding site selection. Cues signifying suitable habitat might differ by sex and change with individual age (e.g., Hoelzer 1987). Since the behavioral processes associated with each type of habitat selection are similar, I will focus on breeding site selection. The presumption here is that regardless of life-stage, sex, season, or activity, an individual will select habitat to maximize its expected fitness within the restrictions met in natural settings, and that this selection is based on an internal template and recognition system (Fig. 1).

Breeding site selection

Cues of habitat quality might be associated with direct or indirect measures of food availability or particular habitat features, or be evaluated indirectly using conspecifics or heterospecifics as cues (Table 1). The template shape and threshold placement can be modified subsequently based on breeding experience (e.g., Reed & Oring 1992). Baker (1978) created a simple model for animal movements that he applied to all movement decisions, including breeding site selection, whereby an individual's movement decisions could be thought of as a series of thresholds, consistent with recognition system template thresholds, driving the decision to stay at a site or to move on. Ketterson and Nolan (1983) criticized this as a general model for movement decisions, suggesting that there is no physiological reality associated with the cascading series of thresholds, and that the suitability of potential breeding sites probably is a continuum of quality from which an individual selects the best point. These two ideas are compatible within a recognition system framework (Fig. 1). For example, breeding site quality might be a continuum for some species, or it might be a continuum modified by a bivariate cue (e.g., presence or absence of a suitable cavity for a species that is an obligate cavity nester). Regardless, when an individual arrives at a site, it can compare that site to a template of suitability, and the site can be rejected or accepted

(Fig. 1). This decision can be made using any of a number of selection rules, such as the best-of- n sites sampled, or selecting the first site that surpasses some minimum standard. These types of models are common in mate-selection and foraging theory (discussed in Reed *et al.* 1999), and there are additional related models of prospecting for breeding sites (e.g., Johnson 1989, Boulinier & Danchin 1997), that might lend themselves well for modification to a recognition system framework. Manipulating potential cues of habitat suitability, as has been done for colonially nesting birds (*see* section 'Facilitating habitat selection'), could be used to determine which cues are most important for site selection and where thresholds in the template exist.

Cue perception and action is central to recognition systems, and cues might differ between males and females, or by life stage. For example, spotted sandpipers (*Actitis macularia*) are sequentially polyandrous, and female fitness is associated with the number of mates acquired in a season (Oring *et al.* 1991). Territory site selection by older individuals is partly affected by nesting success or failure in previous years, and when both potential mates have had prior success on different territories pairing can be delayed because of conflict over territory site selection (Oring *et al.* 1994). Males assess reproductive success by number of their own chicks fledged, while females base it on number of eggs laid (Oring *et al.* 1994), and information on local

Table 1. Examples of cue types for breeding site selection.

Cue Type	Taxon	Example citations
Food	widely exhibited by invertebrate herbivores	Chew (1988), Jaeniki & Papaj (1992)
Habitat structure	widely exhibited by birds	Wiens (1989), Marshall & Cooper (2004)
Conspecifics	widely exhibited by birds beetles, diptera spiders	Stamps (1988, 1991), Reed <i>et al.</i> (1999) Grevstad & Herzig (1997), Onyabe & Roitberg (1997) Samu <i>et al.</i> (1996), Hodge & Storfer-Isser (1997), Schuck-Paim & Alonso (2001)
	marine invertebrates lizards mammals	Scheltema <i>et al.</i> (1981), Burke (1986), Minchinton (1997) Stamps (1987, 1988, 1991) Hoeck (1982, 1989), Weddell (1991)
Heterospecifics	spiders	Hodge & Storfer-Isser (1997)
	birds	Mönnkönen & Forsman (2002), Thomson <i>et al.</i> (2003)

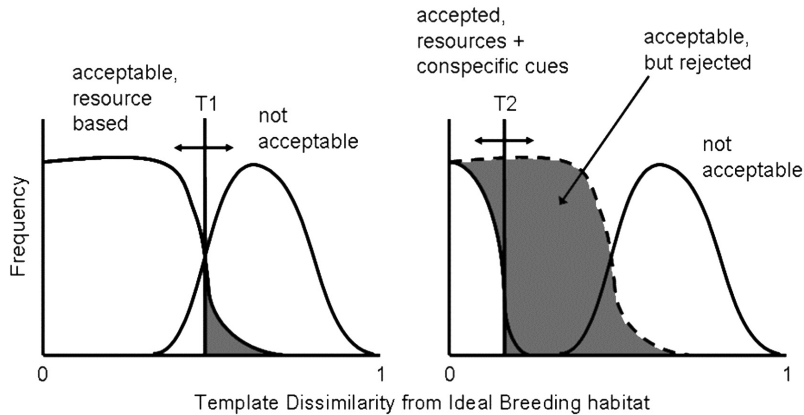


Fig. 2. Schematic of a recognition template for breeding site selection depicting acceptable and unacceptable habitat based on resources needed for breeding and the threshold for rejection (T1), with rejection errors shaded (left), and acceptable habitat based on resources needed plus a conspecific cue for settling, with the revised threshold for rejection (T2) (right). The shaded area represents habitat that is rejected but would be acceptable based on resources needed for breeding. Axes as in Fig. 1.

reproductive success affects settlement (habitat selection) of prospecting females in subsequent years but not of prospecting males (Reed & Oring 1992).

The availability of multiple cues of habitat quality allows for the possibility of a greater range of rejection errors if the cues are obligate (or strongly favored) rather than facultative. For example, sites might exist that are functionally suitable for breeding (e.g., available breeding site and food) that are rejected because they lack an indirect cue of suitability such as presence of conspecifics (Fig. 2). There is a growing body of research in animal behavior investigating the availability and use of public versus private information, or cues, in breeding site selection (Serrano *et al.* 2001, Doligez *et al.* 2003, 2004, Pärt & Doligez 2003). Private information is available only to the individual and comes from personal experiences. Public information includes cues that are generated incidentally by the behavior of another individual, thus becoming available to observers. For example, by selecting a breeding site an individual provides a cue to conspecifics, and sometimes to heterospecifics (Table 1), about the potential suitability of adjacent sites. This information can be gathered during prospecting, when individuals sample potential breeding sites and use the information for subsequent breeding site selection, sometimes more than a year later

(Reed *et al.* 1999). In fact, the easiest time to determine what might be the template for habitat selection could be during population recovery (if population decline was unrelated to habitat loss) or when there is abundant newly created or restored habitat. Prospecting individuals in a setting where there is abundant suitable habitat available would be expected to select the best habitat. Although the literature and language pertaining to “public cues” have not crossed over to species conservation, the concepts have been applied extensively. The availability of public cues provides opportunities to manipulate behavioral cues of breeding habitat selection for species conservation (*see* section ‘Facilitating habitat selection’), thus manipulating local population dynamics and demography (Ray *et al.* 1991, Reed & Dobson 1993, Boulinier & Danchin 1997, Reed & Levine [in press]).

Because recognition templates and threshold placements are the result of evolved processes and individual experience, the introduction of exotic, invasive species can increase the rate of discrimination errors. Exotic invasive species are a leading cause of species extinction (Wilcove *et al.* 1998), and negative effects on endemic species often occur through competitive displacement or depredation. However, exotic species can have more insidious effects associated with recognition behavior and breeding site selection. For example, the green-veined white butterfly

(*Pieris napi*) native to eastern North America has undergone a range reduction and local declines are occurring (Chew 1981). *P. napi* oviposits on plants of the Brassicaceae, and are being impacted by the invasion of garlic mustard (*Alliaria petiolata*), a *Brassica* species that produces a chemical cue (a type of glucosinolate) that signals acceptability to these butterflies for ovipositing (Louda & Mole 1991). Unfortunately, *P. napi* caterpillars have high mortality on *Alliaria* because they cannot metabolize one of the plant's defense chemicals (Courant *et al.* 1994). Interestingly, *P. napi* in Europe develop normally on *Alliaria* (Bowden 1971). Recognition conflicts are found in other species of Pierine butterflies in the presence of other species of exotic invasive host plants (Bowden 1971, Chew 1977, 1981, Chew & Renwick 1995). I suspect this type of recognition system disruption in native species is common where exotic species invade, and if the result of the recognition error is severe enough, native species making the recognition error either will evolve or go extinct. For further discussion of recognition systems and invasion success, see Starks (2003) and Payne *et al.* (2004).

Dispersal

After individuals are born (or whatever taxon-specific equivalent occurs), there eventually is the necessity to reproduce. If reproduction occurs any place except where the individual was born, there is dispersal to that new site, and many species have some active form of dispersal and breeding site selection (Clobert *et al.* 2001). Recent research related to species conservation has shown that dispersal is increasingly difficult as habitats become fragmented (e.g., Cooper *et al.* 2002). Dispersing individuals that are not traveling in a random direction or through Brownian motion appear to have some sort of template regarding habitat suitability during dispersal because they disperse through certain types of habitat and avoid others. Although these selections might be physiologically based for some species, such as avoiding dehydration by not crossing open habitat, it is becoming clear that for some vertebrates that dispersal

habitat selection and avoidance is behaviorally based (Harris & Reed 2002). Dispersal and other movements in birds are well studied, particularly in forest birds. Song or alarm call playback has been used to study movement, taking advantage of responses to cues for competitors or predators, and researchers have shown that many forest bird species avoid crossing gaps on forest habitat (Desrochers & Hannon 1997, Rail *et al.* 1997, St. Clair *et al.* 1998). The response appears to be graded by distance, with decreasing likelihood of crossing larger gaps (e.g., Rail *et al.* 1997, Harris & Reed 2002). These results are readily explained by the existence of a template of varying degrees of dispersal habitat acceptability with thresholds related to distances beyond which individuals will not cross.

Facilitating habitat selection

If we can recognize the cues used by different species to determine the level of habitat suitability, the cues can be manipulated to achieve conservation goals (Reed & Dobson 1993, Reed 2002). Hunters have used cues, in the form of decoys and calls, for centuries to draw species to habitats (e.g., Kear 1990). In fact, hunters as a group have employed to some degree experimental protocols based on recognition behavior to refine the cues being used by species for site selection. A recent example of this is ROTODUX, a white, horizontal plastic cylinder with longitudinal blades, where the cylinder is spun using an electric motor (<http://www.rotoducks.com/>) and the spinning/flashing motion attracts waterfowl to feeding sites. This "display" acts as a strong stimulus for attracting waterfowl to foraging sites. An example from hunting and conservation biology is the use of nest boxes to attract cavity-nesting species to areas from which they had been absent, with excellent examples coming from waterfowl (Kadlec & Smith 1992) and eastern bluebirds (*Sialia sialis*) (Zeleny 1977). As creation of artificial nesting sites for conservation purposes expands (e.g., Lalas *et al.* 1999, Stamp *et al.* 2002), it will require a better understanding of species-specific nesting cues and templates. Breeding cue manipulation has been particularly effective in seabird conservation.



Fig. 3. Laysan albatross decoys in courtship pose at Kaohikaipu, an island in Waimanalo Bay, Oahu, Hawaii. (Photograph courtesy of Mark Rauzon, Marine Endeavors, Oakland, California).

Decoys and/or sound recordings of colonies have been used to induce colonially nesting seabirds to establish new breeding colonies for least tern (*Sterna antillarum*) (Kress 1983) and Atlantic puffin (*Fratercula arctica*) (Kress 1978, Kress & Nettleship 1988), and to attract wading birds to foraging sites (Crozier & Gawlik 2003). Using decoys as a cue to attract birds was taken further in the Laysan albatross (*Diomedea immutabilis*), where breeding site selection cues were refined by providing decoys of chicks and of adults in courtship poses (Fig. 3) (Podolsky 1990). The use of breeding cues has been effective for other types of birds as well. Endangered black-capped vireos (*Vireo atricapilla*) were attracted to new breeding sites using territorial song playback (Ward & Schlossberg 2004), and dispersing griffon vultures (*Gyps fulvus*) were attracted to abandoned breeding sites by spreading white paint to simulate conspecific feces (Sarrazin *et al.* 1996). Although manipulating breeding cues has not been tried for invertebrate conservation, I suspect taking advantage of aggregation and reproductive hormones, as is done for pest control (*see* section ‘Pest deterrence and control’ below), could be a useful species conservation technique.

Clearly, understanding the recognition cues used by threatened species for breeding site, non-breeding site, and dispersal habitat selection would be a valuable resource for effective habitat restoration. Experiments to determine which

cues are most important in attracting animals or triggering breeding would be an effective application of recognition behavior to species conservation. The use of artificial attractants shows promise. Some hunting organizations are concerned that new electronically driven technology being used to attract waterfowl might be so effective that it might result in long-term declines of waterfowl populations (e.g., California Waterfowl Association, <http://www.calwaterfowl.org/Currentevents37.htm>). Using similar technology to generate cues for species conservation could be a boon. Currently the use and refinement of this type of behavioral manipulation for species conservation lags behind use for hunting. It should be noted, however, that there is a potential danger in attracting individuals to a site if this site is actually inappropriate for breeding and creates an attractive population sink (Delibes *et al.* 2001).

Mating success

Hybridization, or introgression, between species or subspecies might be thought of as a mate recognition error (Rhymer & Simberloff 1996, Buerkle *et al.* 2003). Hybridization is regular but infrequent, particularly if you base species designations on the biological species concept (Mayr 1966). By definition hybridization is uncommon because sympatric species have evolved isolat-

ing mechanisms, such as elaborate displays or species-specific cues, to prevent hybridization. In recognition systems this involves the refinement of a mate selection template and appropriate placement of the rejection threshold (*see* Göth & Hauber 2004, Lewis *et al.* 2004). Under some conditions, however, hybridization can become more common: (a) when species become rare, the acceptance threshold for mates can shift, probably because the real risk of not encountering an acceptable mate could result in reproductive failure (Reeve 1989); hybridization can be a particularly acute problem for captive populations; (b) when habitat changes allow formerly allopatric species to become sympatric through range shifts and interspecific isolating mechanisms do not exist; and (c) when exotic species are introduced to a new geographic region and

reproductive isolating mechanisms do not exist (Table 2). The second and third scenarios would be exacerbated when populations are small (scenario a); that is, when we are most worried about extinction risk. Under all scenarios, a species either will evolve isolating mechanisms, improving their mate recognition template and shifting their rejection threshold, or it might go extinct if humans do not successfully eliminate the exotic species. For example, the koloa (Hawaiian duck) (*Anas wyvilliana*) shows signs of going extinct through introgression with mallards (*A. platyrhynchos*) (Browne *et al.* 1993, Rhymer 2001). Mallards have been found on the Hawaiian Islands since at least the late 1800s. Recent surveys show that koloa might exist only as hybrids on Oahu and Maui, and hybrids have been found on Kauai and the Big Island, islands

Table 2. Examples of species and subspecies that are threatened by introgression.

Threatened species or subspecies	Hybridizing with	Citations
Catalina mahogany (<i>Cercocarpus traskiae</i>)	Mountain mahogany (<i>C. intricatus</i>)	Rieseberg & Swensen (1996)
Cutthroat trout (<i>Oncorhynchus clarki</i>)	Rainbow trout (<i>O. mykiss</i>)	Meyer <i>et al.</i> (2003), Weigel <i>et al.</i> (2003)
Shortnose sucker (<i>Chasmistes brevirostris</i>)	Smallscale sucker (<i>Catostomus rimiculus</i>) and Lost River sucker (<i>Deltistes luxatus</i>)	Tranah <i>et al.</i> (2003)
Cuban crocodile (<i>Crocodylus rhombifer</i>)	American crocodile (<i>C. acutus</i>)	Ramos <i>et al.</i> (1994)
Guanay cormorant (<i>Phalacrocorax bougainvilli</i>)	King cormorant (<i>P. albiventer</i>)	Bertellotti <i>et al.</i> (2003)
European quail (<i>Coturnix c. coturnix</i>)	Japanese quail (<i>C. c. japonica</i>)	Deregnaucourt & Guyomarch (2003)
Koloa (<i>Anas wyvilliana</i>)	Mallard (<i>A. platyrhynchos</i>)	Browne <i>et al.</i> (1993), Rhymer (2001)
White-headed duck (<i>Oxyura leucocephala</i>)	Ruddy duck (<i>O. jamaicensis</i>)	Hughes (1996)
Black stilt (<i>Himantopus novaezelandiae</i>)	Pied stilt (<i>H. himantopus</i>)	Pierce (1984)
Forbe's parakeet (<i>Cyanoramphus forbesi</i>)	Red-crowned parakeet (<i>C. auriceps</i>)	Nixon (1994), Triggs & Daugherty (1996)
European wildcat (<i>Felis silvestris silvestris</i>), Sardinian wildcat (<i>F. s. libyca</i>)	Domestic cat (<i>F. s. catus</i>)	Daniels & Corbett (2003), Pierpaoli <i>et al.</i> (2003)
Dingo (<i>Canis lupus dingo</i>)	Domestic dog (<i>C. familiaris</i>)	Daniels & Corbett (2003)

previously thought to contain only pure koloa (Swedberg 1967, Engilis *et al.* 2002). Because koloa show no evidence of changing their mate selection criteria, at least at a pace sufficient to maintain the koloa as a species, there is a fear that in the absence of a rapid and strong human response the koloa will become extinct in the near future (Engilis *et al.* 2002).

A contrasting viewpoint on hybridization can be constructed, however. Mate selection involves selecting the best mate an individual can get in a particular situation. If an individual finds itself in a site with no potential mates of the same species, it can either court the individuals available or try to find a site with conspecific mates. If the individual stays, then hybridizing is the best available option. Whether or not this is an "error" in an evolutionary sense depends on the result of mating. If viable offspring are produced, then the mate selection might not be considered an error. In the example of Geospizid hybrids given above, hybridization does not result in reduced reproductive output, and the young produced are as viable as those from conspecific matings (Grant & Grant 1992). Consequently, hybridization is apparently not an error from an evolutionary perspective, although under normal settings of mate availability conspecifics are selected as mates.

When population size gets too small, one effect that has been observed in some species is a sharp decrease in reproductive success (e.g., Kuusaari *et al.* 1998). Reproductive behavior in some species is stimulated by external cues, such as pheromones or social stimulation (e.g., Stacey *et al.* 2001). Manipulating cues to increase reproductive activities in small populations could stimulate population growth. The examples provided above for generating new seabird colonies demonstrate this. As another example, Pickering and Duverge (1992) stimulated pre-reproductive displays in a captive flamingo (*Phoenicoinais* spp.) flock by putting up mirrors to give the appearance of more individuals. Work on giant pandas (*Ailuropoda melanoleuca*) shows an important role of chemical signaling in sexual motivation (Swaigood *et al.* 2003), which suggests chemical cues might be manipulated to stimulate breeding. In fact, female mating preference for particular males has been manipulated

by altering odor cues for familiarity (pygmy loris, *Nycticebus pygmaeus* (Fisher *et al.* 2003)) and for male quality (harvest mice, *Micromys minutus* (Roberts & Gosling 2004)). Similar preference manipulation has been done by altering visual cues in zebra finches (*Poephila guttata*) with extraordinary results. Burley (1986a) showed that the color of plastic leg bands placed on males could double reproductive success for birds banded with "attractive" colors, (Burley 1986b), alter the sex ratio of offspring to favor the "attractive" mate (Burley 1986a, 1986c), and increase mortality rates for "unattractive" birds (60% vs. 13% for "attractive" birds during the time of the experiment; Burley 1985). Although mating preference or reproductive success responses to color band cues are observed in some other bird species (Hagan & Reed 1988), it is not universal (Weatherhead *et al.* 1991, Cristol *et al.* 1992). Color bands are not the only cue that can be altered to manipulate mating preferences. Adding novel traits, such as a colored feather to a bird's head, or altering colors on a bird can affect mate choice (Witte & Curio 1999, Witte *et al.* 2000, Collins & Luddem 2002). Females evaluating males based on non-personal cues, such as nest site ornamentation (e.g., Ostlund-Nilsson & Holmlund 2003), broadens the possibilities of manipulating mate attraction. Although novel ornaments do not cause universal response across species (e.g., Horster *et al.* 2000), it suggests that there is broad opportunity to manipulate mating cues to achieve conservation goals, including maintaining genetic variability in a population.

Maintaining genetic variability

Loss of genetic variability can threaten species persistence by increasing the expression of deleterious alleles and by the loss of potential for evolution (Allendorf & Leary 1986, Frankham *et al.* 2002). Important factors determining the rate at which genetic variability is lost from a population include mate selection and reproductive output (Parker & Waite 1997). In particular, the more skewed the breeding sex ratio, and the more skewed the variance in individual reproductive success, the more rapidly allelic

diversity is lost. Consequently, increasing the proportion of individuals breeding and reducing variance in reproductive success among individuals maximizes effective population size (N_e ; an index of the rate of loss of genetic variability; the larger the N_e , the slower the rate of loss) (Falconer 1989). Blumstein (1998) and Reed (2002) used simple modeling scenarios to show the degree to which manipulating mate preference and relative reproductive success among individuals might increase N_e . This could be done by manipulating mate-selection cues (previous section). Genetic variability also could be increased through immigration, and the methods described above to increase dispersal or colonization (*see* section 'Facilitating habitat selection') could be used to increase genetic variability.

Manipulating mate preference and relative reproductive success among individuals, however, might not provide a net conservation benefit. (1) Genetic variability is not inherently beneficial to a population. If there are a large number of lethal equivalents in the resident population, or if introducing immigrants disrupts local adaptations, the resulting population might have reduced fitness. (2) Evolution favors individuals that select superior individuals as mates. Encouraging a more even mating success among individuals could result in a population with poorer mean fitness. Since the genetic makeup and functional relationships of genes are not known for most individuals or species, and are unlikely to ever be known, one might argue that manipulating breeding behavior and gene pools cannot be done effectively. This may not be the case. There are ecological indicators of inbreeding depression, such as lower-than-expected reproductive output, that might indicate benefits to manipulating the population's genetic structure.

Self incompatibility genes

A fine example of a recognition based mating system problem comes from self incompatibility genes, which are common in flowering plants (Richards 1997, also discussed by Payne *et al.* 2004). In small populations, self-compatibility alleles can be lost through genetic drift (Frankham *et al.* 2002), resulting in low com-

patibility among individuals in the population, which is a type of Allee effect. Demauro (1994) describes a situation in which a population of endangered lakeside daisies (*Hymenoxys acaulis*) had grown so small that reproduction did not occur. Eventually plants were fertilized by pollen from another population. It is not clear how this recognition system restriction could be bypassed, beyond importing breeders or reproductive propagules, but it exists as a conservation challenge.

Predator avoidance

Predator recognition is a learned trait in some species, and lack of recognition or discrimination by captive reared individuals can be a problem when they are released into the wild (Griffen *et al.* 2001). Predator recognition also is a problem in natural populations when predators are reintroduced or naturally recolonize an area from which they are absent and local prey no longer respond appropriately to the predators (Berger *et al.* 2001, Lima 2002). Predator recognition cues and appropriate discrimination might be entrained in naïve individuals. For example, rufous hare-wallabies (*Lagorchestes hirsutus*) have been trained through exposure to live predators (McLean *et al.* 1994, 1995), and predator models have been used to train wild and captive-reared endangered species to recognize predators and to respond appropriately (e.g., Takahe, *Porphyrio mantelli* (Bunin & Jamieson 1996), New Zealand robin, *Petroica australis* (McLean *et al.* 1999)).

There is an extensive body of work investigating predator recognition that is being done to address problems unrelated to species conservation, including work on chemical cues of predator presence (e.g., Mirza & Chivers 2000, Blumstein *et al.* 2001, Burns & Wardrop 2001, Griffin *et al.* 2001, Berejikian *et al.* 2003, Leduc *et al.* 2004). Goals of this recognition system based research include determining which specific cues and contexts elicit different types of anti-predator responses, and more practical problems such as increasing survivorship of hatchery raised fish for recreational fishing. This body of work might provide experimental protocols for refining behavioral training for predator recogni-

tion and discrimination for threatened species conservation, as might aversion training and learning from psychological studies (*see* next section 'Pest deterrence and control'). In particular, gaining a better understanding of the predator presentation context that elicits the quickest and most effective response would be important. This might include, for example, creating superstimuli or more effectively negatively reinforcing simulated predator encounters.

Pest deterrence and control

It might seem odd to cover pest deterrence and control in a paper on species conservation, but some endangered species are considered pests by some people (e.g., gray wolves, *Canis lupus* (McNay 2002)), and pests can threaten the persistence of endangered species. In both situations, recognition behavior can play, or has played, a role in species conservation. Approaches for controlling vertebrate and invertebrate pests has taken advantage of recognition behaviors for a long time, particularly for controlling agricultural pests. Invertebrate pests, such as Japanese beetles (*Popillia japonica*) can be drawn to a site using aggregation or sex pheromones and at that site they can be killed or exposed to pathogens (e.g., Klein & Lacey 1999, Symonds & Elgar 2004; *see* Pedigo 2001 for a review of management techniques for invertebrate crop pests). Some vertebrate pests are controlled using behavioral cues, such as stool pigeons and Judas goats, whereby an animal's aggregation behavior is used to trap other individuals. The current manifestation of the Judas goat technique to capture or kill feral goats (*Capra hircus*) involves releasing animals with radio collars into the area targeted for goat control. Goats are social animals that aggregate, so after a sufficient period of time the radio-collared animals are located and goats in that group are killed (Keegan *et al.* 1994). This technique is now being used on feral pigs (*Sus scrofa*) (McIlroy & Gifford 1997). Sometimes humans taking advantage of aggregation behavior can be extremely effective, as it was partially responsible for the extinction of passenger pigeons (*Ectopistes migratorius*) and Carolina parakeets (*Conuropsis carolinensis*), both of which were perceived as crop pests (Schroger 1955, McKinley 1985). The techniques used to control species perceived as pests often need to be developed through trial and error (or better yet through strong inference and experimental procedures) for each species. For example, attempts at European starling (*Sturnus vulgaris*) deterrence appear to be largely ineffective or effective only for the short term (Belant *et al.* 1998). However, lessons learned from controlling one pest might be extended to other pests, as with the examples just given.

Another area of pest control research that involves recognition behavior is the use of taste aversion agents. This approach involves conditioning a predator's behavior by treating baits or mock prey (e.g., an egg) with an emetic compound such as lithium chloride, to stop unwanted depredation. The use of conditioned taste aversion to prevent depredation appears to have limited and inconsistent success (Smith *et al.* 2000), and an ideal agent for conditioned taste aversion has not yet been developed (Gill *et al.* 2000). A related type of aversion training is the use of chemical or acoustic repellants or deterrents, which also are used to repel herbivores (Horn 1983, Lehner & Horn 1985, Nolte 1999). Visual and acoustic stimuli seem to be effective for only a limited time (Belant *et al.* 1998, Smith *et al.* 2000), although based on years of biomedical research on aversive conditioning to noxious stimuli this result is not surprising (citations in Romero 2004). Animals also might be repelled using recognition associated with scent marking. Because mammalian predators respond to individual scents (e.g., Hutchings & White 2000), there is the potential to create mock predator territories in high-risk or high-conflict areas to repel endangered predators. In addition, if prey respond to predator scents (e.g., Downes & Adams 2001, Kusch *et al.* 2004), scents might be used to keep threatened prey species away from high-risk areas. These ideas rely completely on the understanding and manipulation of recognition systems.

It might be of value to systematically review the pest control literature from the point of view of recognitions systems theory. That is, one might identify cues for attraction or repulsion, determine if there are taxonomically or eco-

logically based patterns, isolate what part of each cue type is most responsible for the action, and use this to come up with a 'theory of pest control' that could be applied to new pests. Using deductive reasoning to make the leap between species-specific solutions and broader patterns seems like an important use of recognition systems theory.

Conclusions

Recognition behavior is central to many aspects of species conservation, in understanding, solving, and sometimes inadvertently creating problems. Much of what I presented in this review shows the early state of scientific development in addressing behavior-related problems in species conservation. This was not intended to be a complete review of the topics presented, and there are other topics in recognition systems that could affect conservation strategies or offer a means to manipulate a species' behavior, such as food (prey) selection. For example, it could be particularly important for species where adult food selection is affected by experiences early in life (Distel & Provenza 1991), or if food selection can be culturally transmitted (Mirza & Provenza 1990, Thorhallsdottir *et al.* 1990). One observation I can make from this review is that there are important lessons and approaches to be drawn from basic research and from applied research on domestic and hunted species.

Conservation biologists are always hoping to discover a new box of tools for solving specific problems in species conservation. Recognition systems do not come with a ready set of tools for this purpose, but based on this review, it is clear that recognition systems show promise as a research framework for refining study of the behavioral issues important to species conservation. In particular, (1) recognition systems predict variability among individuals in preferences and in behavioral responses to the same stimulus, and it predicts thresholds in behaviors (Fig. 1). Both of these patterns are observed in natural populations, and might provide a behaviorally based framework for population phenomena such as critical thresholds in habitat occupancy associated with habitat cover (e.g., Homan *et al.*

2004). (2) Recognition systems emphasize the importance of an evolutionary perspective for thinking about problems, and this is important in species management and conservation (e.g., Gavin 1991, Ashley *et al.* 2003). (3) And recognition systems emphasize the hypothesis-driven approach to problem solving that has been advocated for improving the effectiveness of wildlife management (e.g., McNab 1983, Davis 1985, Murphy 1990). Finally, this review reinforces the continuing importance of understanding the natural history of species that are targets of conservation activities, either to protect the species, or to remove the species because it is a threat (Schrader-Frechette & McCoy 1993, Grant 2000, Dayton 2003).

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