The action component of recognition systems: a focus on the response

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The action component of recognition systems is concerned with the response of an evaluator to perceived cues, based on the dissimilarity of those cues compared with a template. Building upon the historical focus on kin recognition, we apply the framework of conspecific acceptance thresholds to recognition in a broader sense, including interactions within and between organisms, between species, and between living and nonliving things. We review examples from a variety of taxa and recognition contexts to demonstrate when a discriminatory response is expected, and how this response may be flexible depending on the costs and benefits of recognition errors and the interaction rate with cue-bearers in a given environment. Investigation of response flexibility must incorporate natural and life history data as well as controlled laboratory studies whenever possible in order to separate flexibility due to perceptual differences from shifting acceptance thresholds.

Introduction

Two decades after Hamilton introduced the concept of kin selection (Hamilton 1963, 1964a, 1964b), studies of kin recognition began to receive a great deal of attention (*see* reviews in Fletcher & Michener 1987, Beecher 1988, Blaustein 1988, Waldman 1988, Gamboa *et al.* 1991, 1996, Hepper 1991a, Pfennig & Sherman 1995, Sherman *et al.* 1997, Mateo 2003, Holmes 2004). Almost all of this early work explored mechanisms designed to facilitate nepotism or to avoid inbreeding, and thus focused only on recognition between conspecifics (i.e., between parents and offspring, among siblings or other group members, and between potential mates; *see* fig. 1 in Göth & Hauber (2004)). Although the conceptual framework and associated language used by different investigators originated from a variety of subjects (e.g., inclusive fitness theory, signal detection and communication theory, and cognitive psychology), many of these parallel lines of research converged upon similar ideas about recognition systems (Appendix).

Despite the focus of attention on conspecific interactions and nepotism, the process of recognition plays an essential part in virtually all interactions among animals. In his introduction to a symposium on recognition at the 1980 Annual Meeting of the American Society of Zoologists, Beecher (1982) noted the importance of recognition at many levels, from discrimination of unique individual signatures within a dominance hierarchy to the more general identification of conspecifics. To further extend this idea, we can think of recognition systems as relevant for interactions
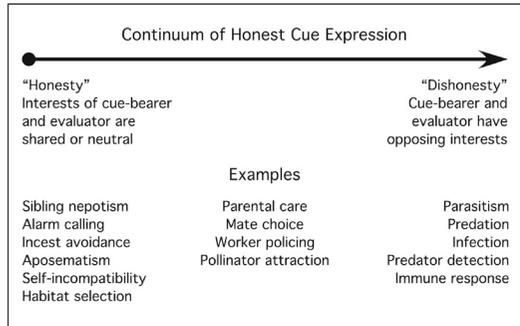
Continuum of Honest Cue Expression

"Honesty"
Interests of cue-bearer
and evaluator are
shared or neutral

"Dishonesty"
Cue-bearer and
evaluator have
opposing interests

Examples

Sibling nepotism
Alarm calling
Incest avoidance
Aposematism
Self-incompatibility
Habitat selection

Parental care
Mate choice
Worker policing
Pollinator attraction

Parasitism
Predation
Infection
Predator detection
Immune response

Fig. 1. Continuum of honest cue expression depending on overlap of interests between the evaluator and cue-bearer in given recognition context.

within as well as among individuals, and between organisms and abiotic factors in their environment. Thus we can apply the same conceptual framework to understand processes as seemingly diverse as cell recognition, sibling cooperation, predator detection, and habitat selection (Alexander 1979, Sherman *et al.* 1997).

Definition of terms

The process of recognition requires two participants, which have been called many different names over the history of recognition system research (Appendix). Because many of these original studies focused only on kin recognition, they tended to use terms that implied interaction of two animals. The main difference in terminology arose from whether authors focused on the individual doing the recognizing or the individual bearing the cues to be recognized (e.g., "actor" *vs.* "recipient" of Reeve (1989), Sherman *et al.* (1997); "receiver" *vs.* "signaler" of Beecher (1982, 1989); and "discriminator" *vs.* "target" of Tang-Martinez (2001)). However, our broader view of recognition systems does not specify taxonomic origin of the participants; neither does it exclude interactions at a cellular level or between biotic and abiotic factors. We therefore will introduce the term "evaluator" for the recognizing participant and use the term "cue-bearer" introduced by Fletcher (1987) for the entity being recognized, whether living or non-living. These terms are inclusive of recognition systems at all levels and generate less

confusion than other terms in implying active *vs.* passive participation.

The system by which the evaluator may recognize the cue-bearer consists of multiple components, which also have been broken down and named in a variety of ways since studies of recognition systems began (Appendix). Despite the differences in terminology, authors have generally agreed that recognition systems must include (1) a set of cues produced by the cue-bearer, (2) perception of these cues by the evaluator, and (3) potential discriminatory response by the evaluator. These three steps have been termed the expression (*see* Tsutsui 2004), perception (*see* Mateo 2004), and action components (*see* Sherman & Holmes 1985, Reeve 1989, Sherman *et al.* 1997; Appendix). The separation of these three components can help investigators isolate and test both proximate and ultimate hypotheses relating to the complex process of recognition, and thus we will adopt these terms in our review.

Three components of recognition systems

The expression component refers to the presence and development of cues expressed by the cue-bearer (reviewed by Tsutsui 2004). The cues used in recognition have also been called traits, labels, and signals (Appendix), but they all refer to the fact that there must be a stimulus that is perceived by the evaluator. Depending on the context, selection may favor anything from honest expression to "scrambling" of cues by the cue-bearer. Honest expression of cues is expected when the evaluator and cue-bearer have common interests or when the cue-bearer is "neutral" regarding recognition. In contrast, cue-scrambling is expected when the interests of the evaluator are in opposition to those of the cue-bearer (Fig. 1). The expression component thus emphasizes the importance of the cue-bearer as a 'participant' in the recognition process. (As stated earlier, participant, in our usage, does not necessarily suggest an animate object.) The perception component involves the sensory detection and processing of cues by the evaluator via comparison with a template. The development of this template is also part of the perception com-

ponent (reviewed by Mateo 2004). Thus, the first two components are concerned primarily with the proximate mechanisms that allow recognition to occur. Finally, the action component refers to the response of the evaluator given the similarity between cues and template. The decision rules and subsequent actions (or lack thereof) that comprise the response are more relevant to an ultimate, or functional, perspective; if the evaluator is able to respond to the presence of cues due to selection on the expression and perception components, the appropriate response by the evaluator (the action component) will depend on the adaptive significance of discrimination in that context (Holmes & Sherman 1983, Waldman 1987, 1988, Reeve 1989, Beecher 1991, Gamboa *et al*. 1991). Selection is thus expected to act on all three components (Beecher 1991), each of which is a necessary part of the process of recognition.

Focus on the action component

In this paper, we will review the theory and empirical evidence regarding the action component of recognition systems. Because the recognition system framework can be applied to such an immense range of interactions, we obviously cannot present a comprehensive review. Rather, we will focus on several examples that demonstrate the range of possible recognition contexts in a variety of taxa. It is important to note that an evaluator's response can be physiological/developmental or behavioral (Gamboa *et al*. 1991, Sherman *et al*. 1997). Although we will focus the majority of our review on behavioral responses, there are many interesting examples of recognition-induced developmental/physiological changes.

One such example occurs in red-eyed tree frogs (*Agalychnis callidryas*). Warkentin (1995, 2000) has presented clear evidence that these frogs can alter the timing of their development in response to environmental cues signifying imminent danger. Specifically, the frogs are able to shorten their embryonic development time by hatching early in response to predation by snakes and wasps, or by the presence of harmful fungus. Each of these threats expresses different cues,

so frog embryos must recognize them separately and respond accordingly. Interestingly, although vibrational stimulation resulting from wasp and snake predation is the cue for early hatching, frog embryos do not hatch indiscriminately to vibrational stimulus, i.e., they don't hatch during egg mass collection or due to earthquakes or storms. Thus the embryos are able to recognize and respond developmentally to environmental cues that indicate the presence of a specific threat.

Another example of a developmental response to recognition can be found in amphibian larvae that sometimes develop a cannibalistic phenotype. Pfennig and colleagues have studied this phenomenon in spadefoot toads, which develop in temporary ponds that are at risk of drying before the tadpoles can complete their development. Although the tadpoles all start life as omnivores, consumption of other tadpoles or fairy shrimp can trigger changes in morphology and dietary preference that result in an exclusively carnivorous phenotype (Pfennig & Sherman 1995). In one study of this system, Pfennig and Frankino (1997) raised tadpoles of two species of spadefoot toads on an omnivorous diet including fairy shrimp and rabbit chow. They found that *Spea multiplicata* tadpoles were less likely to develop a cannibalistic phenotype when raised in pure sibship groups than in mixed sibship groups, and that *S. bombifrons* tadpoles were less likely to develop a cannibalistic phenotype when raised in pure sibship groups than when raised alone. Another example from a similar system comes from the salamander *Hynobius retardatus*, in which broad-headed cannibal "morphs" were also less likely to develop when in the presence of close kin, even at high densities when this morph is more commonly produced (Michimae & Wakahara 2001). These examples illustrate that the action component of recognition systems need not be restricted to behavioral changes in the traditional sense.

Acceptance threshold framework

As mentioned previously, much of the early work on recognition systems focused on identification of relatives for nepotism or optimal outbreeding.
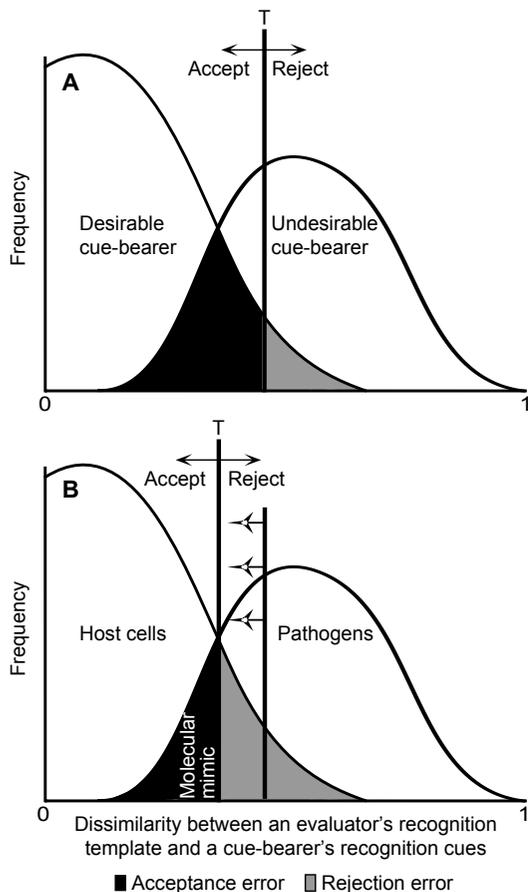
Fig. 2. — **A**: Hypothetical frequency distributions of dissimilarity between an evaluator's recognition template and an encountered cue-bearer's recognition cues. 'T' is the threshold above which cue-bearers are rejected and below which they are accepted. — **B**: Indicates a shifted threshold within the context of an immune system response. The area shaded in black indicates pathogens with cues that overlap with desirable cue-bearers ("molecular mimics") and are accepted by the host cells.

The development of ideas about response thresholds were therefore based mainly on the goal of matching phenotypes of classes of relatives to an inner recognition template (Getz 1981, Holmes & Sherman 1983, Lacy & Sherman 1983, Crozier 1987; *see* Mateo 2004 for discussion of template formation). Getz (1981) introduced a formal framework for understanding such a mechanism in which evaluators compare the similarity of their own cues with the cues of others with whom they interact. He developed a graphical method called a "kingram" for comparison of cue distributions for different classes of relatives and for calculation of an optimal decision rule to minimize recognition errors. Reeve (1989) further developed the idea of evolutionarily stable acceptance thresholds for conspecific recognition, showing how optimal discrimination thresholds can evolve based on the relative costs and benefits of discrimination in a given interaction context (Appendix). Specifically, if an evaluator has a binary choice to either accept or reject a cue-bearer, the optimal acceptance threshold should depend on the relative benefits of accepting and rejecting desirable and undesirable cue-bearers, the costs of making acceptance and rejection errors, and the rates of interaction with desirable and undesirable cue-bearers. The threshold should always be more restrictive with increasing cost of accepting undesirable cue-bearers, but the effects of interaction rates are likely to differ depending on the type of recognition context (i.e., a "guard" evaluator that can accept multiple cue-bearers *vs.* a "searching" evaluator that must seek out cue-bearers and make a greater commitment to acceptance). Reeve modified the kingram developed by Getz into the cue dissimilarity distribution to graphically represent these ideas (Fig. 2A).

To illustrate how this framework may be used for systems other than recognition of conspecifics, consider the identification of harmful pathogens by the immune system. If the cue dissimilarity distributions of the body's own cells overlap with that of an undesirable pathogen, we would expect the threshold for immune response to be based on rates of interaction with that pathogen, and the relative costs of mounting an unnecessary immune response against desirable cue-bearers *vs.* failure to attack a potentially harmful pathogen. A threshold that is too restrictive could result in auto-immune disease, while an overly permissive threshold would expose the body to damage by the pathogen (Fig. 2B). Note that the actual template used by the evaluator, whether an antigen-specific receptor in the immune system or a neural representation within an animal's brain, is not relevant to our focus on the response threshold.

Within this framework, thresholds are expected to become more permissive as costs of

rejection errors increase relative to acceptance errors. An example of a shift to more permissive thresholds due to the relative cost of rejection errors can be seen in the facultatively polygynous ant *Pseudomyrmex pallidus*. Starks *et al.* (1998a) found that although *P. pallidus* workers could discriminate nestmates from non-nestmates, workers from polygynous colonies (i.e., colonies with more than one queen) were less aggressive toward non-nestmates (i.e., made more acceptance errors) than workers from monogynous colonies (i.e., colonies with a single queen). This is expected according to the acceptance threshold model because workers in polygynous colonies would be exposed to greater genetic diversity of nestmates, and would therefore have broader template distributions of desirable cues. This would lead to greater overlap between desirable and undesirable cue-bearers, and thus a shift toward a more permissive threshold is expected to balance the cost of acceptance and rejection errors.

Another example of how social context can affect optimal thresholds occurs when mothers and offspring reunite in a communal nursery setting, or crèche. In this situation common to many birds and mammals, parents benefit by accurately locating and feeding only their own offspring while the offspring benefit from receiving care from any adult (Beecher 1991, Keller 1997, Holmes 2004). Thus it is expected that parents will have a greater cost of acceptance errors than offspring, who will have more permissive thresholds than their parents as they both attempt to reunite within the crèche. This asymmetry is also consistent with theory regarding parent-offspring conflict from an inclusive fitness perspective, whereby parents have "less to lose" by the death of an offspring (that shares half the parent's genes) than the offspring's loss of its own life (Trivers 1974). In support of this idea, Insley (2001) found asymmetrical vocal recognition errors between mothers and offspring of the northern fur seal *Callorhinus ursinus*. In this species, mothers returning from foraging trips must reunite with their offspring among a group of hundreds or thousands of conspecific pups. Vocal playback experiments showed that mothers and offspring were both able to recognize each other's vocalizations, but that pups had more "false alarms" (acceptance errors) than the mothers. The optimal threshold for mothers and offspring in such a situation may also depend on their physiological or developmental state (i.e., hunger, age, sex) and the costs of recognition errors (from the pup's perspective, starvation *vs.* aggression from unrelated adults).

More restrictive thresholds are expected as costs of acceptance errors increase relative to rejection errors. Consider the example of nest guarding by mole rats. Cooney (2002) found that subordinate Damaraland mole rats (*Cryptomys damarensis*) differed from subordinate naked mole rats (*Heterocephalus glaber*) in their willingness to attack same-sex intruders. Damaraland subordinates, who do not breed in the natal colony due to inbreeding avoidance, are less likely to attack intruders than dominants, who monopolize breeding. Thus, the costs of acceptance errors are extremely high for dominants, who are therefore more restrictive than subordinates in their willingness to accept intruders. In contrast, subordinate naked mole-rats are able to inherit the dominant breeding position in the natal colony and thus have more at stake and more restrictive thresholds (i.e., they are more willing to attack intruders) than Damaraland subordinates. The more restrictive threshold for dominant breeders relative to subordinates is also present in *Polistes* paper wasps. In *P. fuscatus*, the female that dominates egg-laying within a cooperative group of nest-founding females has been found to respond more aggressively to individuals attempting to enter the nest than subordinate members of the group (Fishwild & Gamboa 1992, Gamboa 1996, 2004).

Because so many factors can affect the costs and benefits of recognition errors for a given individual and we often cannot know the shape of the relevant cue dissimilarity distributions, precise calculation of optimal acceptance thresholds may be difficult or even impossible. However, awareness that context is expected to affect optimal thresholds underscores the importance of adequate natural and life history knowledge of study organisms, and allows us to make predictions regarding the expected direction that thresholds should shift with changing contexts. The studies described above illustrate how such life history information can be successfully used

to make and test predictions for their respective study systems using the recognition system framework.

No action ≠ no recognition

In previous work on recognition systems, the term "discrimination" has frequently been used to distinguish the action component from "recognition", which was limited to the mechanisms of the expression and perception components (e.g., Waldman 1987, Tang-Martinez 2001). However, "discrimination" does not fully capture the range of possible responses that must be considered part of the action component. When a behavioral action is consistently observed in response to a given cue (i.e., discrimination occurs), we infer that the evaluator is able to recognize the cue. But how do we interpret a lack of discrimination?

Evolutionary lags and template exploitation

Lack of discrimination behavior may indicate that the existing expression (cue characteristics) or perception (mechanism or internal template) components of the interaction are insufficient for recognition by the evaluator. For example, the template may not have evolved a response to the cues produced by a recently introduced predator or parasite. The sudden increase in brood parasitism by brown-headed cowbirds (*Molothrus ater*) in recently fragmented habitat may exemplify this type of problem for forest bird species (Hosoi & Rothstein 2000).

Because the evaluator's internal template is based on cues displayed by desirable cue-bearers or their environment (*see* Mateo 2004), the template may consequently be incapable of distinguishing between predators or parasites that mimic desirable cue-bearers and the desirable cue-bearers themselves. This may explain the successful usurpation of host colonies by *Polistes* wasp social parasites (*see* Gamboa 2004). The queen of the parasite *P. atrimandibularis* mimics the odor of the host species *P. biglumis*, but the parasite's offspring have

parasite-specific odors (Lorenzi 2003). The host workers are unable to discriminate between their own and the parasite species, which makes sense if they learn to recognize colony signatures after emergence on a nest filled with both host and parasite offspring (Pfennig *et al.* 1983). This also appears to be the case for some male *Photinus* fireflies. Males signal in flight to females and, if females respond, the male joins the female on the ground. Unfortunately for the male, predatory females of the genus *Photuris* have evolved the ability to mimic the species-specific *Photinus* female response call. In the latter case, the male does not mate with the female but instead is consumed by her (*see* Lewis *et al.* 2004).

Universal acceptance

Alternatively, lack of discrimination does not necessarily indicate lack of recognition; rather, the particular costs and benefits of the recognition context may result in an optimal threshold of universal acceptance or rejection (Holmes & Sherman 1983, Reeve 1989, Beecher 1991, Gamboa *et al.* 1991, Keller 1997, Starks *et al.* 1998b, Starks 1999). A universal acceptance rule might be adaptive in a situation where the relative cost of accepting an undesirable cue-bearer is much lower than the cost of rejecting a desirable cue-bearer, or if the frequency of interaction with undesirable cue-bearers is very low compared to desirable cue-bearers. For example, Blatrix and Jaisson (2002) looked for kin discrimination in queenless colonies of the ant *Gnamptogenys striatula*, where workers transport males inside the colony to mate with other workers displaying "sexual calling" postures. They found no evidence for kin discrimination, and suggested that since inbreeding is very unlikely under natural conditions due to male dispersal and female philopatry, universal acceptance may be favored.

Another context in which universal acceptance may be optimal is parental recognition of offspring in a natal nest when the likelihood of interacting with undesirable cue-bearers is extremely low. This low risk of acceptance error would be expected in solitary-nesting animals with little chance for offspring to accidentally end up in the wrong nest, but it also may occur

in social species before the offspring are mature enough to leave the nest and risk mixing with unrelated individuals. Such a universal acceptance rule explains the ease of cross-fostering young offspring of many vertebrates with parental care (Hoogland & Sherman 1976, Holmes & Sherman 1982, Beecher 1988, 1991, Loesche *et al.* 1991).

Universal rejection

At the opposite extreme where the costs of accepting an undesirable cue-bearer and/or interaction rates with undesirable cue-bearers are very high, universal rejection may be adaptive. For example, female moorhens (*Gallinula chloropus*) that have not begun to lay eggs will destroy any eggs they find in their nest; this occurs in monogamous pairs as well as in communal nests (McRae 1996). Thus, moorhen females use knowledge of their own egg-laying behavior to set the acceptance threshold; after they have begun laying, the increased risk of destroying their own offspring shifts the threshold to become more permissive.

Similarly, for a social species with inbreeding avoidance, individuals may be expected to reject all mating attempts while in the context of the natal nest where potential partners are likely to be siblings. This is often given as an explanation for sex-biased dispersal in many social animal species. For example, superb fairy-wren *Malurus cyaneus* females demonstrate universal rejection of breeding opportunities while in the natal territory. They always disperse before breeding, even when the resident breeding male is not a genetic relative due to extra-pair fertilization (Cockburn *et al.* 2003). Cooperatively breeding acorn woodpecker groups also demonstrate incest avoidance behavior (Koenig *et al.* 1999, Haydock *et al.* 2001). Helpers in these groups refrain from reproducing when their parents or close relatives hold breeding status. An interesting conflict arises when a breeding vacancy occurs and same-sex, nonbreeding helpers are present; the advancement of the helper to breeding status would result in incestuous mating, but allowing an unrelated immigrant to fill the vacancy would severely limit the helpers' chances for future reproduction. Groups with such vacancies have been observed to refrain from breeding for as long as 3.8 years (Koenig *et al.* 1999). Thus two conflicting rules of universal rejection — avoidance of breeding with relatives, and rejecting immigrant joiners by same-sex helpers in the breeding queue — leads to decreased reproductive success of groups with such vacancies. Interestingly, rejection of incestuous mating is not always universal in acorn woodpeckers, but the observed exceptions have occurred only when male helpers are present and a male breeding vacancy occurs. Haydock *et al.* (2001) interpret these findings as potentially arising from different ecological constraints on dispersal of male *vs.* female helpers. Thus contextual differences may result in a shift toward more permissive thresholds for males compared to females. Further investigation of possible contextual differences among male helpers would be helpful for understanding why some males have more permissive thresholds for incestuous mating than others in apparently similar situations.

For many contexts, the lack of discrimination clearly cannot be used to infer an inability to recognize. Indeed, as the acceptance threshold model is based in part on the relative fitness costs of acceptance and rejection errors, our current empirically supported theoretical construct specifically predicts an absence of discrimination in contexts in which recognition may occur. Alternatively, lack of discrimination may result from a lack of recognition. In cases of mimicry, for example, the ability to discriminate may be far too costly to evolve. Using our autoimmune disease example, if immune system acceptance thresholds were sufficiently restrictive to identify molecular mimics, the likely outcome would be an increase in rejection of self. In this case, lack of recognition (and discrimination) is selectively advantageous. Not all similar failures of recognition will be advantageous, of course, as was made clear with our brood parasite examples.

How then to tease apart the potential causes for the lack of discrimination? A general understanding of the expression and perception components may indicate when, for a specific context, the non-discriminated participant's cue diversity is either successfully mimicked or sufficiently novel to result in a lack of recognition. Perhaps

the best test is to examine recognition behavior in multiple contexts: as the relative fitness costs of acceptance and recognition errors may change in different contexts, lack of discrimination in one context may not be observed in another (*see* Starks *et al*. 1998b). However, as perception is an internal process, showing that lack of discrimination is accompanied by a lack of recognition (or by the ability to recognize) may not occur until advances in neurophysiological methods render common the study of the neurobiology of recognition. Fortunately, increasing interest in collaboration between the fields of behavioral ecology and neurobiology will undoubtedly lead us closer to this goal (Hauber & Sherman 2001, Bekoff & Sherman 2004).

Response plasticity and context-dependence

Acceptance thresholds are sometimes referred to as either fixed or flexible. In addition to expected shifts in fixed thresholds over evolutionary time as cue dissimilarity distributions and rates of interactions with recipients change, Reeve (1989) suggested that selection should favor flexibility of acceptance thresholds *within* the same individual for different contexts where these same factors vary. In the attempt to categorize recent empirical evidence of acceptance thresholds as fixed or flexible, we found that "context-dependence" and "flexibility" were often difficult to define because these terms have been applied both to changes in the ontogeny of the template that determines the response and to the response itself, which confuses the perception and action components of recognition. It is therefore important to distinguish between flexibility in the recognition template and flexibility in the acceptance threshold. In a given recognition system, the evaluator's response might differ depending on whether the template is static (i.e., is determined genetically or via "imprinting") or updatable (i.e., can change to incorporate new information about desirable or undesirable cue-bearers). Yet the response may also differ according to whether the threshold is fixed (i.e., the acceptable level of dissimilarity from the template does not change) or flexible

(i.e., threshold can shift to become more permissive or restrictive depending on context). We will address each of the four possible combinations produced by this scheme, and will suggest examples that illustrate the specific characteristics of each scenario.

Static template, fixed threshold

The most stable type of response is expected when an evaluator has both a static template and a fixed threshold. This situation is most likely to occur when cue dissimilarity distributions have minimal overlap and cues are stable over time. This may be particularly applicable to species recognition or sex recognition in sexually dimorphic species. For example, male Japanese swallowtail butterflies *Papilio xuthus* recognize females suitable for mating by using photoreceptors on their genitalia to identify the presence or absence of female genitalia (Arikawa *et al*. 1997). Because the cue is either present or absent, there should be minimal overlap in distributions of male and female cues regardless of context, and thus a fixed threshold would be expected.

Fixed thresholds and static templates may also be expected in a mate choice context when costs of searching for mates are high (Real 1990). A study of mate sampling behavior by female sand gobies demonstrated support for this idea (Forsgren 1997). Half of the females were observed to spawn with the first male they encountered, and none were observed to return to a previously encountered male. Forsgren concluded that they were using a fixed threshold decision rule, and suggested that this may be due to potentially high predation risks for conspicuously colored female sand gobies searching for mates away from shelter. However, Forsgren also found that thresholds became more restrictive later in the season, so the fixed threshold might only apply at the start of the breeding season. In general, fixed threshold decision rules for mate choice may be optimal only when search costs are high, the pool of possible mates is large, and evaluators have accurate knowledge of the distribution of mate quality (Luttbeg 2002). When evaluators have limited time or information, or

the pool of potential mates is small, a decision rule that allows for comparison of relative mate quality or allows for updating of information (e.g., "best-of-*n*" or "Bayesian updating" rules) may be a better option than a fixed threshold (Luttbeg 2002).

A complication of identifying a static template, fixed threshold scenario may occur when templates are determined via imprinting at an early age, resulting in different (but fixed) responses for individuals reared in varying environments. An example of this can be seen in the response by Belding's ground squirrels to conspecific alarm-calls to warn of nearby predators. Mateo and Holmes (1999a, 1999b) found that individual squirrels developed different thresholds of response to conspecific alarm calls based on whether they were reared in the wild or in captivity. These differences persisted even though the current context of the study was captivity; thus the template for the alarm-call and threshold for response were set at an early age based on rearing environment. Although later studies found inter-individual differences in acceptance thresholds based on rearing environment, *within* individuals both the template and the threshold were fixed.

Updatable template, fixed threshold

Responses may change over time due to incorporation of new information into the template representing a desirable cue-bearer, without necessarily requiring any change in the acceptance threshold. This situation could be misinterpreted as a flexible threshold because of different responses for individuals across contexts, when in fact only the template itself has been altered and the acceptable level of dissimilarity between the cue-bearer and the evaluator's internal template has not changed. We might expect to find such a situation when relevant cues for a desirable cue-bearer change over time, but the costs of recognition errors and distributions of desirable and undesirable cue-bearers do not change. However, if the perception component allows for refining of the template and presumably increased accuracy in recognizing desirable cue-bearers, it may be unlikely that the acceptance

threshold would be restrained to a fixed point and therefore unable to take advantage of this new information.

One way that this situation may be relevant in recognition systems is when, rather than shifting a general acceptance threshold to accommodate one internal template, evaluators develop separate templates and thus separate (fixed) thresholds for different individuals (*see* Thom & Hurst 2004). For example, a study of Richardson's ground squirrels found that individuals updated their thresholds for response to alarm calls based on the reliability of the individual caller in previous situations (Hare & Atkins 2001). In this case, the evaluators formed individual templates for different callers as more information about their reliability became available over time. The threshold for response could then be fixed for different cue-bearers because of an updated template. The flexibility in this situation occurs within the perception component; the ability for these squirrels to store information about multiple individuals allows greater accuracy in setting separate response thresholds for action, without necessarily requiring shifting acceptance thresholds.

Static template, flexible threshold

Responses may differ because of shifting acceptance thresholds while the template itself is not updated. This situation might be likely when the cues involved in the template are stable over time, but the interaction rate with desirable and undesirable cue-bearers or the cost of recognition errors fluctuates. An example of this may occur in the context of mate choice where, as mentioned previously, evaluators with limited time or information may do best to modify their acceptance thresholds based on new information gained in the search for mates. Evidence for this has been found in the variable field cricket *Gryllus lineaticeps*. Virgin females of this species are known to prefer males with higher chirp rates, but Wagner *et al.* (2001) showed that females' response to a low chirp rate call varies depending on their previous exposure to either low or high chirp rates. Specifically, females were divided into two groups and exposed to a sequence of

three calls; both groups were exposed to a low chirp rate for the first and third calls, but group two was exposed to a high chirp rate for the second call while group one heard a low chirp rate. The results showed that group two females were less responsive to the low chirp rate in the third call than group one females that had never heard a high chirp rate call. The females exposed to the high chirp rate may have shifted to a more restrictive threshold as predicted for some searching contexts (Reeve 1989) where the interaction rate with desirable cue-bearers increases and the cost of acceptance errors (i.e., mating with a low quality male) is high.

The clearest examples of static templates and flexible thresholds may be in contexts where the cue-bearer is inanimate, such as in many cases of habitat selection (*see* Reed 2004). For example, Seeley (1977) has shown that scouts of the honey bee *Apis mellifera* have a clear preference for certain cavity characteristics, which they then express via a dance on the reproductive swarm (*see* also Seeley & Buhrman 1999). These characteristics relate to the size of the cavity, the size of the entrance, and the distance from the daughter colony. While an optimal cavity certainly exists, honey bees will select sub-optimal nesting sites when rushed to a decision by rain or when the swarm's energy stores are insufficient for the required search time. Accordingly, while the template of an ideal nest site may be fixed, the threshold for acceptance of nesting sites will vary with context.

Appropriate examples of flexible thresholds and static templates come from social insect guards allowing entrance of nestmates *vs.* nonnestmates into the colony. In the paper wasp genus *Polistes*, workers develop templates for nestmate recognition based on colony-specific odors that are learned after emergence from the pupal stage (*see* review in Gamboa 2004). These workers perform foraging duties off the nest as well as on-nest duties such as offspring care and colony maintenance. It is reasonable to expect that thresholds for acceptance of non-nestmates should be more restrictive in the context of the natal nest. This is because the cost of behaving tolerantly to a non-nestmate that has entered the evaluator's nest is likely to be far greater than the same level of tolerance while foraging. A non-nestmate intruder may attempt to usurp the nest or steal brood. Indeed, Starks *et al.* (1998b) found evidence to support this prediction; *P. dominulus* wasps were more aggressive in the presence of cues signifying proximity to the nest than when such cues were absent. In an excellent demonstration of threshold flexibility through short term changes in the nest guarding context, Downs and Ratnieks (2000) showed that nest entrance guards of the honey bee *Apis mellifera* shifted their acceptance threshold of conspecifics as nectar availability changed. As nectar increased, the amount of robbing decreased and thus the cost of accepting an undesirable cue-bearer decreased; eventually universal acceptance was observed.

Updatable template, flexible threshold

The most dynamic type of response is expected when evaluators can incorporate new information into templates in addition to shifting their acceptance thresholds depending on the context. We might expect this situation to occur among social organisms where evaluators have access to continuous information about changes to their environment. In the previous social insect examples, for instance, it is possible that colony-specific odors actually change over the course of the nesting season and thus colony members must update their templates for nestmate recognition (Gamboa 1996). This may occur because of queen turnover (Klahn & Gamboa 1983, Klahn 1988, Van Hooser *et al.* 2002), or incorporation of environmental odors from food or nesting material into the colony signature (Pickett *et al.* 2000). Thus the template itself must keep changing with changing conditions, and the acceptance threshold is also expected to differ according to the environmental context as described in the previous section.

The differences in the last three scenarios may sometimes be subtle — the perception and action components especially tend to become difficult to untangle in examining context-dependent discrimination (Gamboa *et al.* 1991) — however, this confusion serves to demonstrate the integrated nature of the components of recognition systems, despite our attempts to separate them

into definable categories. Future directions for research on the action component of recognition systems will need to integrate knowledge of all components in formulating predictions for expected behavioral responses. Of major importance for the specific examination of acceptance threshold flexibility is the gathering of natural and life history data on study species. Others have pointed out (e.g., Waldman 1988, Beecher 1991, Blaustein *et al*. 1991, Gamboa *et al*. 1991), and we agree that researchers must understand the natural contexts which their study subjects are expected to encounter over the course of their development in order to make predictions and design reasonable experiments to address these issues.

Conclusions and future directions

We have attempted to show the wide applicability of the recognition system framework for predicting responses of evaluators to cues in different behavioral and ecological contexts. Although exact prediction of optimal thresholds may be difficult or impossible for a given system without full knowledge of the shape of cue dissimilarity distributions, this framework provides a helpful basis for generating hypotheses regarding relative differences in expected thresholds. We expect that shifting thresholds will accompany changes in benefits to accepting and rejecting cue-bearers, relative costs of making acceptance and rejection errors, and interaction rates with desirable and undesirable cue-bearers. Thus we can make predictions for relative differences in evaluators' acceptance thresholds across species, populations, and individuals. Because detailed knowledge of relevant life history information is more likely at smaller scales, we suggest that such hypotheses are most informative at the level of the individual evaluator within a particular population. This includes changes in thresholds *among* evaluators exposed to different distributions of cue-bearers, as well as *within* evaluators over time and across environmental contexts.

One obvious needed course of action is to determine the true shape of the cue dissimilarity distributions for desirable and undesirable cue-bearers. While this seems an extraordinarily
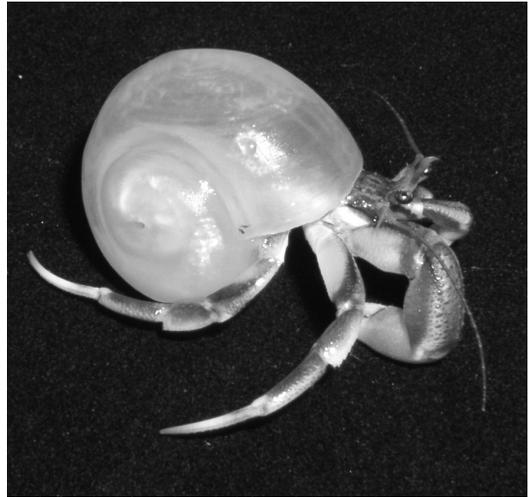

Fig. 3. Hermit crab (*Pagurus longicarpus*) in an artificial shell (Gravel *et al*. 2004). Photo courtesy of Jan Pechenik.

complicated task, some simple systems may lend themselves well to this form of research. Take, for example, shell selection behavior in hermit crabs. With new computer-based shell fabrication technologies, it has become possible to generate shells that differ in minute ways (Gravel *et al*. 2004). Since hermit crabs will discriminate between these fabricated shells based on producible characteristics, it may be possible to manufacture an ideal shell, that is, a shell that exactly fits a hermit crab's template (Fig. 3). Once the characteristics of the ideal template have been identified, then the characteristics of natural shells that are accepted and rejected can be used to calculate the respective cue dissimilarity distributions. While this research is far from straightforward and extremely time-intensive, it represents a possible avenue for determining cue dissimilarity distributions.

Another example of how this framework can be used to advantage in designing laboratory studies comes from the field of biological control of invasive species (*see* Payne *et al*. 2004, Reed 2004). Using the stimulus-response framework of cognitive psychology, Barton Browne and Withers (2002) discuss some potential problems with the design of host specificity tests for feeding and oviposition by parasitoid wasps intended as biocontrol agents. They review data that show how the physiological state of the

study subject (time since last feeding or oviposition) and the context of the test (no choice, sequential choice, simultaneous choice) can affect the acceptance threshold of different hosts, thus leading to potential errors in interpretation of recognition ability and host preference. In this system, understanding the adaptive benefit of shifting thresholds in a given context may aid understanding of the mechanism by which hosts are selected. As suggested by Keller (1997), an interesting direction of this type of research is to test predictions regarding selection on cue-bearers to "scramble" their cues, preventing accurate recognition by the evaluator. This is expected in asymmetrical contexts such as parent–offspring recognition, worker policing, infection, predation, and parasitism, where the discriminator and cue-bearer have different or even opposing interests (Fig. 1). Thus the focus on adaptive value of discrimination leads us to reconsider adaptive value for the cue-bearer to obscure recognition.

Although some may argue that the framework we have presented is too broad, we believe that this is exactly the reason it is beneficial. This framework is inclusive of multiple approaches, and the use of a common language among physiologists, behavioral ecologists, and cognitive psychologists may allow better integration and communication of ideas among researchers working at different levels of analysis.

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Appendix. History of theoretical advances in the study of recognition systems. Columns indicate the work cited, categories and terms used for participants and components of recognition, and brief synopsis of ideas raised by the authors. References are presented in chronological order, except where more than one paper is cited for the same author and similar points were made in both references.

Reference	Participants	Components	Recognition system concepts introduced or discussed by authors
Alexander and Borgia 1978, Alexander 1979	No general terms used	In terms of genetic recognition: 1. Perceptible feature of phenotype 2. Perception of feature 3. Appropriate social response	• Two classes of nepotism suggested: 1. Discriminative: tolerate/help only individuals that meet certain criteria (relatives or reciprocating individuals). 2. Nondiscriminative: either always tolerate/help or never tolerate/help all individuals encountered; most likely to help when chance of accidentally helping nonrelatives is negligible. • Kin discrimination framed in terms of acceptance/rejection by comparison of phenotypes; comparison of phenotypic overlap would not lead to intragenomic conflict as would recognition based on a particular gene. • Drew parallel between mechanisms of nepotism and those of immune system, but suggested that immune response is more comparable to responses toward predators, prey, parasites, or symbionts than toward conspecifics.
Getz 1981	No general terms used	1. Labeling system 2. Recognition (acceptance/rejection)	• Introduced "kingrams" to graphically obtain minimum error decision rules for kin and group recognition. • Demonstrated greater efficiency of genetic-based recognition in haplodiploid *vs.* diploid organisms. • Showed that few loci w/several alleles are adequate for recognition; also suggested that kingrams could be based on phenotypic characters that are not single-gene products.
Beecher 1982	Receiver and sender	1. Identification (signal) 2. Recognition (decoding) 3. Action (signature-matching process)	• Discussed recognition as simple communication system with sender and receiver. • Stated that identification process had previously been neglected in favor of recognition process; focused primarily on signatures and specified 3 cases for identification of sender: *Requires prior contact:* 1. Critical period for learning signatures while contextual info is present; signatures later used when contextual info is absent; selects for many unique signatures because so many potential recognition errors. *No prior contact:* 2. Common, acquired signature such as maternally provided label. 3. Similarity of different genetically inherited signatures, where relatedness is correlated with signature similarity.

Appendix. Continued.

Reference	Participants	Components	Recognition system concepts introduced or discussed by authors
Holmes and Sherman 1982, 1983	No general terms used	1. Proximate (mechanistic: "how") 2. Ultimate (evolutionary: "why")	• Argued that lack of discrimination should be understood as proximate *vs.* ultimate levels of analysis; lack of discrimination ability may be due to lack of selection for this ability. • "Failures" to identify kin discussed in light of evolutionary history of social interaction; recognition is not expected between historically non-interacting classes of individuals. • Developed "phenotype matching" mechanism of kin recognition, comparing it to "stimulus generalization" concept in psychology.
Lacy and Sherman 1983	Observer and observee (and referent for development of template)	1. Traits 2. Template or phenotype-matching	• Modeled "phenotype matching" mechanism of recognition of three classes of diploid conspecifics: full siblings, half siblings, and nonrelatives, using self or parents as referents. • Matches were more accurate with continuously varying traits than discrete ones, but environmental variation increased the rate of recognition errors to a greater extent for continuous traits. • For discrete traits, many loci or multiple traits were necessary for accurate recognition.
Sherman and Holmes 1985	Observer and observed individual	1. Production 2. Perception	• Introduced terminology for production and perception components of kin recognition.
Gamboa 1986	No general terms used	1. Expression 2. Perception	• Pointed out underestimation of importance of environmental components of recognition cues; argued that selection should not act exclusively on genetically-based cues if environmental cues also provide information about kinship, and supported this with a model. • Suggested environmental recognition odors could help maintain uniformity of colony-specific cues, especially if genetic diversity is increased via multiple queens or multiple mating. • Developed "scented candle" model of long-lasting odor production via permanent "trapping" of environmental odors into cuticle of newly emerged wasps. • Grouped adaptive contexts of nestmate recognition into "guard" and "search" categories, and provided evidence for cue-similarity threshold model of nestmate recognition in social wasps. • Discussed possible preadaptive contexts for the evolution of recognition ability in solitary and social wasps, including mate choice, nest recognition, and parent-brood recognition.
Blaustein *et al.* 1987	Target individual and sender	1. Display of cues 2. Receipt of cues 3. Motor response	• Pointed out that phenotype matching and recognition allele mechanisms may be impossible to separate experimentally, and may even be part of the same mechanism. • Suggested that kin recognition behavior is polymorphic, i.e. there is variation in expression of recognition behavior within populations or experimental groups, and this can be maintained by changing environments and selection pressures. • Noted that recognition behavior can vary within an individual depending on environmental conditions. • Recommended that studies be done in both lab and field, then replicated with large sample sizes and in different populations because of plasticity in recognition behavior.

Reference	General terms	Components	Description
Crozier 1987	No general terms used	Not explicitly discussed	• A unity of mechanisms for learning kin cues (template development) is suggested, as there is often a period of learning during a "protected" phase where new individuals learn the cues from referents in the group or existing group members learn cues of newcomers. • Genetic polymorphism for kin discrimination cues may be maintained because of selection on existing genetic recognition systems for pathogen immunity, incest avoidance, parent-offspring recognition, or individual recognition in dominance hierarchies.
Fletcher 1987	Discriminating individual and cue bearer	1. Cues 2. Comparison with template 3. Behavior (cooperative or uncooperative)	• Divided social interactions into cooperative and uncooperative behaviors. Assessment of kin-biased behavior can include both types of interaction. • Variables other than relatedness (e.g., age, sex, health, resource ownership) must be assessed by animals before aiding conspecifics. • Cues used may be intrinsic to the cue-bearer's phenotype, or extended phenotypes of the discriminating individual; multiple cues may be used either simultaneously or sequentially. • Flexible precognition systems are more likely in social groups where constant updating of templates is possible; inflexible "imprinted template" systems are better when relatives disperse but may encounter each other as potential mates later in life.
Michener and Smith 1987	Responding individual and cue bearer (or recognizing individual)	1. Cues or "discriminating substances" 2. Recognition 3. Discrimination	• Distinguished homogeneous from heterogeneous groups, where individuals in the latter type may be individually discriminated rather than united by common cues. • Suggested further study into plasticity of mechanisms for learning kin odors in primitively eusocial insects, and for phylogenetic comparison of behavior divergence in different systems.
Waldman 1987, 1988	No general terms used	1. Labels 2. Templates 3. Decision rules	• Introduced hierarchical framework of recognition mechanisms that may be used concurrently: allelic —> individual —> group. • Mechanisms of kin recognition as points along a continuum rather than discrete processes. • Kin discrimination expected in three categories/contexts: 1. Kin overlap predictably in time and space Initial interaction occurs in reliable context, after which kin can be recognized outside of original setting. 2. Kin encounter each other with no prior or present overlap in temporal or spatial cues.
Reeve 1989	Actor and recipient	1. Production 2. Perception 3. Action	• Introduced term "action component" as third addition to two components of recognition systems described by Sherman and Holmes (1985). • Discussed recognition in terms of conspecific acceptance thresholds; based on cue similarity distributions (modified from Getz 1981 "kingrams"). • Modeled optimal acceptance thresholds, including universal acceptance/rejection, depending on relative costs/benefits of acceptance and rejection errors in particular contexts. Optimal thresholds depend upon on interaction rate with "desirable" and "undesirable" conspecifics, type of recognition system (guard vs. search), and frequency dependence/independence of system.

Appendix. Continued.

Reference	Participants	Components	Recognition system concepts introduced or discussed by authors
Beecher 1991	Receiver and signaler	1. Signature 2. Perception 3. Decision 4. Action	• Warned that discrimination tests should be aware of "detection" vs. "forced choice" designs, because contextual info could affect results and be interpreted incorrectly. • Discussed possibility of selection for recognition signatures.
Gamboa *et al.* 1991	No general terms used	1. Expression 2. Perception 3. Action	• Suggested that other studies' experimental designs had not explicitly recognized or "uncoupled" components, so may have confused which component was being addressed. • Addressed potential biases in discrimination assays and interpretation of negative results. • Stressed that experiments attempting to focus on expression or perception components (i.e., isolation of cues by artificial diet, rearing conditions, etc.) may change context, and thus unintentionally affect action component by changing optimal acceptance threshold.
Hepper 1991	Receiver and sender	1. Cues 2. Ontogeny 3. Classification 4. Behavior	• Emphasized role of animal's state (i.e., pregnancy) as part of cues that affect kin recognition along with environmental and conspecific cues. • Response may differ depending on relationship between cues; when conspecific and environmental cues are in "harmony" (i.e., neighbor in home territory) vs. "disharmony" (i.e., stranger in home territory or neighbor outside home territory).
Sherman *et al.* 1997	Actor and recipient	1. Production 2. Perception 3. Action (same as Reeve 1989)	• Reviewed recognition system framework based on Reeve's acceptance threshold model, but wider application than conspecific interaction. • Acknowledged that action component can include behavioral, developmental, and physiological responses. • Suggested broad application of conceptual framework for recognition of cells, individuals, conspecifics (kin, mates, reciprocators, members of hierarchy), heterospecifics (predators, prey, hosts), and habitat.
Tang-Martinez 2001	Discriminator, target, and cue	1. Recognition (mechanism) 2. Discrimination (behavioral response)	• Differentiated between direct and spatially-based "recognition", suggesting that spatially-based discriminatory behavior may result from ancillary effects of kin-biased behavior because of increased fitness due to aggregation with relatives. Inability to discriminate among kin and non-kin in other contexts is actually failure of kin recognition. • Argued that only one true kin recognition mechanism occurs: learning due to familiarity, either directly or indirectly. Difference is only in the cues learned. • Kin discrimination ability likely a by-product of individual, species, or group recognition.
Liebert and Starks 2004	Evaluator and cue-bearer	1. Expression 2. Perception 3. Action	• Expand application of acceptance threshold framework to include interactions within and among organisms, between species, and between living and nonliving things. • Suggest use of terms "evaluator" and "cue-bearer" to allow for variety of systems above. • Discuss types of flexibility and context-dependent responses in terms of development of template (perception) as well as shifting acceptance threshold.