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Recognition systems and biological invasions

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Recognition systems are an integral component of the biology of all species. The highly tuned nature of many recognition systems may make them particularly sensitive to environmental and genetic changes. In this review, we examine how biological invasions influence recognition systems and discuss how plasticity in recognition systems may contribute to the success of species in new environments. Specifically we discuss how demographic and genetic consequences of the invasion process may influence allorecognition, intraspecific, and interspecific interactions. Possible research directions are discussed including the value of comparing species' recognition systems between native and introduced populations.

Introduction

Invasive species can be widespread, have severe environmental impacts (Parker *et al*. 1999, Mack *et al*. 2000) and be economically costly (Wilcove & Chen 1998, Pimentel *et al*. 2000). Despite increased awareness of the effects of invasions, our understanding of how introductions into novel environments change the basic biology of invading species remains poor (Mooney & Cleland 2001).

Recognition is an integral component of many biological systems allowing the discrimination of self from non-self (as in immunological responses) and the identification of different classes of non-self. The ability to distinguish between different classes of non-self allows such widely divergent behaviors as assessing group membership, discriminating in favor of kin, identifying potential prey or predators, attracting conspecifics, choosing mates, and selecting habitat (Sherman *et al*. 1997). Successful recognition requires three components: the *expression* of a signal (reviewed in Tsutsui 2004), the *perception* of the signal by an evaluator (who compares the signal to a template; reviewed in Mateo 2004), and an *action* by the evaluator who may ignore or respond to the signal (reviewed in Liebert and Starks 2004). Templates for recognition can be based on learned cues, and may change with experience during a lifetime, or can be innate (genetically based), and change across generations through selection or drift. Many recognition systems are finely tuned and perturbations that undermine or influence their integrity may be costly.

Recognition systems can be particularly sensitive to environmental or genetic changes that influence any of their components. The establishment of a species in a new area may profoundly affect its recognition system as a result of novel interactions or genetic changes due to founder events and bottlenecks (Mooney & Cleland 2001, Sakai *et al*. 2001, Lee 2002). Biological invasions therefore provide a unique opportunity to examine the selective pressures that affect recognition systems as well as how organisms respond to changes in cues used for recognition. A careful understanding of the recognition systems of invaders may also provide insight into the success of some species.

There is a paradox that bears mentioning. Invading species often contend with reduced genetic variation and compete against locally adapted species in their new range (Allendorf & Lundquist 2003). There also may be costs associated with the breakdown of recognition systems in invasive species. Why, then, are these species such successful invaders if they bear these additional costs?

In this review, we examine how biological invasions influence recognition systems and discuss how plasticity in recognition systems may contribute to the success of species in new environments. In some cases, invasive species succeed in spite of their altered recognition system, while in others, an altered recognition system may contribute to their success (for a review of the conservation implications of recognition systems *see* Reed 2004). Through a series of examples, we examine these questions at the individual (self/non-self recognition), intraspecific and interspecific levels. When appropriate, we also consider the component of the recognition system that has been modified.

Self/non-self recognition

There are many allorecognition systems in which selection maintains a high level of allelic diversity (Grosberg 1988, Richman 2000). Examples include the major histocompatibility complex (MHC) in vertebrates, the sex determination locus in hymenoptera, and self-incompatibility in plants and fungi (Richman 2000, Tsutsui 2004). In all of these systems, the template to which a cue is compared is self, but the resulting action varies. In MHC, self-recognition results in acceptance, while in self-incompatibility systems and sex determination, self-recognition results in rejection. In the context of biological invasions, population bottlenecks may purge many alleles, particularly rare ones (Tsutsui & Case 2001), and if coupled with inbreeding due to demographic limitations, can severely affect these systems.

Histocompatibility complex (MHC)

The multigene family that comprises the major histocompatibility complex in vertebrates is extraordinarily polymorphic (Edwards & Hedrick 1998, Hughes & Yeager 1998). MHC class II molecules bind to and present foreign antigens to lymphocytes, and heterozygosity at these loci is thought to enhance immune function (Doherty & Zinkernagel 1975, Hughes & Yeager 1998). Small population sizes may compromise the integrity of diverse MHC systems, and a population bottleneck (followed by inbreeding) has been implicated in autoimmune deficiencies in the cheetah (O'Brien *et al*. 1983, 1985, May 1995). Biological invasions often result in population bottlenecks, providing an excellent opportunity to examine the consequences of a reduction in allelic diversity at MHC loci. However, unsuccessful invasions are difficult to study (and often go undetected), making a comparison of variation at MHC loci between successful and unsuccessful invasions problematic. Moreover, successful invaders are frequently introduced without their pathogens and parasites (Wolfe 2002, Mitchell & Power 2003, Torchin *et al*. 2003), making it difficult to elucidate the importance of variation at MHC loci in introduced populations relative to native populations. The role of immunocompetence in determining the success or failure of an invasion is an understudied avenue of research that warrants further attention (Lee & Klasing 2004).

Sex determination

Sex in hymenoptera is determined by a single locus at which heterozygotes become females and hemizygotes and homozygotes become males (Crozier 1977). High levels of allelic diversity are necessary for this system to function properly (Crozier 1977, Beye *et al*. 2003). One consequence of reduced genetic diversity or inbreeding in hymenoptera is the production of diploid males. Diploid males are often sterile and if produced in excess, may impose a cost on the colony. Although rare in most social insect populations, they can occur frequently in some introduced species such as polistine wasps (Liebert *et al*. 2004) and have been well documented in North American populations of the red imported fire ant (*Solenopsis invicta*).

The red imported fire ant was introduced into the southeastern United States between 1933 and 1945, probably from northeastern Argentina (Mescher *et al*. 2003). Diploid males are rare in native populations, but can occur at high frequencies (between 70% and 100% of all males) in introduced populations, likely as a result of lost allelic diversity at the sex determining locus subsequent to a genetic bottleneck (Ross & Fletcher 1985, Ross *et al*. 1993). In the field, diploid males occur exclusively in the polygyne (multiple queened) form, although lab monogyne colonies will rear diploid males (Ross & Fletcher 1985). The production of diploid males is costly; colonies with diploid males both delay worker production and produce fewer workers (Ross & Fletcher 1986). Subsequently, diploid male production prevents monogyne colonies from establishing and growing under field conditions. In contrast, polygynous fire ant colonies escape these costs as not all of their queens produce diploid males (Ross *et al*. 1993), and colonies are founded by budding so they begin with a large worker force (Ross & Keller 1995). The high frequencies of diploid males in the U.S. has even led to the production of triploid workers, although no triploid queens have been detected (Krieger *et al*. 1999). Introduced populations of many social insects likely have reduced levels of genetic diversity relative to their native range (Tsutsui & Suarez 2003, but *see* Johnson & Starks 2004). These species may provide an opportunity to examine the origin and consequences of diploid male production across many taxa.

Self-incompatibility

The self-incompatibility locus is common in flowering plants and provides a mechanism by which individuals with the same genotype are prevented from achieving fertilization. There are two types of self-incompatibility, gametic and sporophytic (reviewed in Richman & Kohn 1996). Plants with gametic self-incompatibility (GSI) could propagate if only a single individual was brought to a region, because heterozygotes can still self fertilize. However, such plants remain susceptible to inbreeding depression, or other deleterious effects of reduced genetic variation. In contrast, a single plant with sporophytic self-incompatibility (SSI) would not be able to sexually reproduce if alone because the entire genotype of the pollen donor determines whether fertilization occurs. For a species with this system of mate recognition, at least two individuals would have to be introduced to the same region in order for successful propagation to occur.

A similar self-incompatibility system occurs in many fungi in which mating only occurs between individuals with different alleles at the mating-type locus (MAT) (Kues & Casselton 1992, Marra & Milgroom 1999). Invading fungal species also must contend with recognition of appropriate mating partners or the lack of mates. In some introductions, fungal species can switch from primarily outcrossing to self-fertilization if an appropriate mating type is not present.

In 1905, American chestnut trees, *Castanea dentate*, began dying of a disease caused by the ascomycete species *Cryphonectria parasitica* (reviewed in Anagostakis 1987). Commonly known as chestnut blight, this fungus is native to Japan and China (Shear & Stevens 1913, 1916). Despite the simple self-incompatibility system typical of ascomycetes that would seemingly preclude self-fertilization, *C. parasitica* frequently self-fertilizes in the wild, even in strains that will not self-fertilize under laboratory conditions (Marra & Milgroom 2001, Marra *et al*. 2004). In Marra and Milgroom's (2001) experiment, self-fertilization was not seen in strains of *C. parasitica* from China, suggesting that the ability to circumvent the self-incompatibility system is not common to all geographic regions. More recent work has shown that self-fertilization is common in many introduced populations of *C. parasitica* (Marra *et al*. 2004), while populations in Japan are predominantly outcrossing.

In the case of the chestnut blight fungus, the limitation posed by the incompatibility between identical mating types may be incomplete. In some invasive populations, plasticity in the perception of acceptable mates can lead to an escape from the self-incompatibility system and the ability to reproduce both asexually and sexually. Flexibility in the template corresponding to an appropriate mate may be key to this species' sexual success.

All of these self-referent systems are sensitive to changes in allele number and frequency, and can be compromised by reductions in population size following introduction to a new environment. However, very little information exists on how these systems respond to the genetic and demographic consequence of invasions. Colonization events, also typical of heavily disturbed environments, may reduce the diversity of alleles in a population used for recognition of self/nonself (Richman & Kohn 1999). This can reduce fertilization, lower fitness, and potentially lead to shifts in life history characteristics. Persistence of newly established populations may require the regeneration of allelic diversity, either by mutation or the introduction of new individuals with different alleles. Alternatively, selection may favor a change in the template of what genotypes are accepted as mates. Reconstructing the relationship among alleles at allorecognition loci can be a powerful method to infer changes in population structure (such as bottlenecks) throughout a species' history (Richman *et al*. 1996).

Intraspecific recognition

Recognition is an integral component of conspecific interactions and plays a role in such diverse behaviors as mate choice, territoriality, neighbor recognition, and assessment of group membership in social animals. Recently established populations often occur at low densities and finding mates may be difficult. This may hamper the success of obligately out-crossing species. After establishment, invasive species can achieve remarkably high densities, potentially changing the selective pressures that influence the expression of territorial behavior (through ecological constraints). The process of introduction may also influence the cues used to assess group membership (as with the allorecognition systems mentioned above).

Mating systems

Recently introduced plants and animals must find and recognize appropriate mates if they are to persist in their new environment. Asexuality may enhance the probability of colonization and establishment because of this limitation (Ehrlich 1989, Lodge 1993). Two ways sexually reproducing species may circumvent mate limitation are to become parthenogenic (or change to vegetative growth), or to be less selective and hybridize with closely related species. Notably, asexuality is often thought to arise as a result of hybridization between two sexual species (Vrijenhock *et al*. 1989, Radtkey *et al*. 1995) suggesting that these forces may work in concert to promote the success of some species.

The asexual mourning gecko, *Lepidodactylus lugubris,* is of hybrid origin, and colonized islands throughout the Pacific Ocean likely with the aid of Polynesians about 4000 years ago (Case *et al*. 1994, Radtkey *et al*. 1995). Despite being clonal, *L. lugubris* have fewer parasites than their parental species (Hanley *et al*. 1995) even though they have low levels of diversity at MHC loci (Radtkey *et al*. 1996). However, *L. lugubris* is being displaced on many islands by the recently introduced sexual house gecko *Hemidactylus frenatus* (Petren *et al*. 1993, Petren & Case 1996), suggesting that increased colonization success attributed to asexuality does not translate to increased competitive ability. An examination of why hybridization occurs between some species and how their asexual offspring succeed in new environments may provide insight into the role of mate recognition in the establishment and spread of an invader.

Introduced plants often grow vegetatively, in which genetically identical ramets sprout from a parental unit and extend the physical range of the parent. Genetically identical individuals can invade very large areas (Fahrig *et al*. 1994), as demonstrated by the aquatic fern (*Salvinia molesta*) (Room 1990), and the Japanese knotweed (*Fallopia japonica*) (Hollingsworth &

Bailey 2000). *Fallopia japonica* has become widely distributed in United Kingdom since its horticultural introduction in the 1800s. All plants in the U.K. are male-sterile (Beerling *et al.* 1994) and share identical RAPD profiles (Hollingsworth & Bailey 2000), suggesting that this population may be derived from one ancestor.

The U.K. population of *F. japonica*, if entirely clonal, could be at risk from pathogens as a result of genetic homogeneity. In addition, the plant's inability to produce seed limits its dispersal (Beerling *et al.* 1994). Hybridization with other members of the *Fallopia* genus has restored sexual reproduction and genetic recombination (Hollingsworth *et al.* 1998). Hybrids produce wind dispersed seeds (Beerling *et al.* 1994), representing another mode of dispersal for *Fallopia* species; genetic recombination and more efficient dispersal could lead to even further colonization of the British Isles (Hollingsworth *et al.* 1998).

For hybridization to occur, a species may have to broaden its template and respond to cues from a wider variety of potential mates. It is unknown whether hybridization between closely related taxa occurs more often in introduced relative to native populations. However, two observations warrant further investigation of how changes in recognition systems may lead to increased hybridization. First, introduced plants can hybridize with resident species increasing their invasiveness (Ellstrand & Schierenbeck 2000). Second, parthenogenic species often result from hybridization between sexually reproducing parental species and commonly occur on islands and in disturbed areas (Cuellar 1977, Glesener & Tilman 1978). A careful assessment of mate recognition in both the native and introduced range of invasive species will elucidate the role of plasticity in mate choice in invasion success.

Sociality

The formation of social groups (specifically eusociality) is one of the major transitions in the evolution of life (Maynard Smith & Szathmáry 1995). A careful assessment of group membership is integral for the evolution and maintenance of sociality. Social insects, for example, have well developed recognition systems that are used for distinguishing nestmates from non-nestmates. Colony identity in social insects can be assessed using both genetic and environmental cues (Hölldobler & Michener 1980, Gamboa *et al.* 1986, Breed & Bennett 1987, Hölldobler & Wilson 1990, Beye *et al.* 1998, Breed 1998), and cuticular hydrocarbons are now widely thought to be the label expressing the information needed for nestmate discrimination (Lahav *et al.* 1999, Thomas *et al.* 1999, Boulay *et al.* 2000, Gamboa 2004).

Many species of social insects have established populations outside of their native range, and have become widespread and ecologically destructive (Moller 1996, Holway *et al.* 2002). Social insect recognition systems may be very sensitive to the rapid changes in environmental and genetic contexts brought about by their translocation to a new environment. Invasive ants, for example, can show remarkable variability in social structure between native and introduced populations (Ross & Keller 1995, Ross *et al.* 1996, Tsutsui *et al.* 2000). In the following sections we discuss the recognition systems of some relatively well-studied social insect invaders, and focus on how recognition systems may be influenced by the process of introduction and establishment into a new environment.

Argentine ants

The Argentine ant, *Linepithema humile* (formerly *Iridomyrmex humilis*), is among the most widespread invasive social insects. Established in over 20 countries on six continents (Suarez *et al.* 2001), *L. humile* can have severe impacts on ecological communities, and is a tenacious agricultural and urban pest (reviewed in Holway *et al.* 2002). Throughout its introduced range, biologists have long noted a lack of intraspecific aggression or territoriality among separate nests (Newell & Barber 1913, Passera 1994). This unicolonial colony structure is unusual because nestmate discrimination and territoriality among conspecifics is common in ants (Hölldobler & Wilson 1977, Bourke & Franks 1995). It has been argued that unicoloniality in Argentine ants is a problem for kin selection theory, as queens within nests are thought to be unrelated (reviewed in Bourke & Franks 1995). This "problem for kin selection theory", however, is an artifact of measuring relatedness between individuals within a nest relative to neighboring nests in the same introduced population. Introduced populations of Argentine ants are genetically homogenous relative to populations in their native range (Tsutsui & Case 2001). We get a more accurate sense of the genetic structure of introduced populations when relatedness is estimated relative to the genetic diversity in the native range, where this species evolved (Tsutsui & Suarez 2003). Using this approach, it turns out that relatedness of individuals within colonies in introduced populations can be over 80% (Tsutsui & Case 2001, Tsutsui & Suarez 2003).

The scale over which unicoloniality occurs varies among introduced and native populations of Argentine ants. Throughout their introduced range, intraspecific aggression is typically absent, even among nests separated by hundreds of kilometers (Tsutsui *et al.* 2000, 2003, Giraud *et al.* 2002). In contrast, Argentine ants frequently exhibit pronounced aggression within native populations, and always exhibit aggression among populations separated by a few kilometers (Suarez *et al.* 1999, Tsutsui *et al.* 2000).

Two hypotheses have been proposed to explain differences in the scale at which nest mate discrimination occurs between native and introduced populations (Starks 2003). First, levels of genetic diversity are reduced in introduced relative to native populations of Argentine ants as a result of bottlenecks (Tsutsui *et al.* 2000) and/or frequency dependent selection against novel genotypes (Tsutsui *et al.* 2003). Alternatively, selection against costly aggressive behavior in introduced populations (resulting from ecological constraints) may have changed the threshold at which Argentine ants will discriminate against non-nestmates, leading to a loss of alleles at recognition loci without necessarily reducing overall patterns of diversity at neutral loci (genetic cleansing hypothesis) (Giraud *et al.* 2002).

Based on current evidence, it seems that Argentine ants have not lost their ability to discriminate nestmates from non-nestmates, only that the genetic cues used are more similar among nests in introduced populations relative to native populations (Tsutsui *et al.* 2000, 2003). While this supports the loss of genetic diversity hypothesis, it does not rule out that changes in the threshold at which Argentine ants discriminate nestmates from non-nestmates have also occurred (Giraud *et al.* 2002). Support for this alternate hypothesis will come from a careful comparison of the relationship between nestmate discrimination and the cues used for discrimination in both native and introduced populations. It should also be noted that measuring levels of aggression among nests might miss other subtle forms of discrimination. For example, ants may discriminate nestmates or levels of kin without resorting to aggression, but by modifying the extent to which they share information about resources or fuse nests. Further work comparing native and introduced populations is needed to determine the relative importance of genetic versus environmental cues in nestmate discrimination in Argentine ants.

It has long been suspected that a unicolonial colony structure may reduce the diversity of other ant species (Pontin 1963, Hölldobler & Wilson 1977, Holway & Suarez 2004). The mechanisms behind this displacement may include an increase of interspecific aggression resulting from poor discriminatory abilities (because of extreme polygyny) (Hölldobler & Wilson 1977), higher productivity as a result of having many queens, and the ability to achieve high densities due to a release from costs associated with territorial behavior (Holway *et al.* 1998). Studies conducted under both laboratory (Holway *et al.* 1998) and natural conditions (Holway & Suarez 2004) have provided some evidence that neighboring colonies that are aggressive towards one another have lower resource monopolization rates relative to neighboring non-aggressive colonies. Research is still needed at the population level before this link between colony structure, population density, and competitive ability can be unequivocally established. Also, there is no doubt that if changes in colony structure contribute to the success of invasive social insects, they work in concert with other aspects such as escape from natural enemies, differences in the competitive environment between native and introduced populations, and favorable abiotic conditions typical of the disturbed environments they invade (Holway *et al.* 2002).

Fire ants

Fire ants have two social forms (monogyne and polygyne) that are distinguishable by queen number. The origin of multiple-queen colonies in introduced populations of fire ants was originally attributed to selection for queen adoption into existing colonies, because of ecological constraints on independent colony founding resulting from high densities (Ross & Keller 1995). Recent genetic work has shown that differences in social structure related to queen number can be traced to allelic differences at the general protein 9 (*Gp-9*) locus (Krieger & Ross 2002, reviewed in Bourke 2002, Tsutsui & Suarez 2003). Monogyne colonies have a single queen with a BB genotype while polygyne queens have Bb genotypes. Queens with the BB genotype start colonies independently while Bb queens will stay in their natal nest or join other polygyne colonies. Workers discriminate against queens with genotypes different than their own, preventing the adoption of multiple queens in monogyne nests. Allelic differences corresponding to queen number are conserved among all the species in the South American clade of fire ants (Krieger & Ross 2002). Interestingly, *Gp-9* encodes a protein that shows similarity to an odorant-binding protein (Krieger & Ross 2002), and is over-expressed in workers relative to males and queens (Liu & Zhang 2004). However, Ishida *et al.* (2002) suggest that odor binding proteins should be expressed primarily in the antenna but not throughout the entire ant as appears to be the case with *Gp-9*. Recent work on *Solenopsis geminata* suggests that polygyny in fire ants has evolved through multiple mechanisms because allelic differences at the *Gp-9* locus do not correspond to variation in queen number in this species (Ross *et al.* 2003). An alternate explanation is that the gene or genes responsible for social organization in fire ants are tightly linked with *Gp-9* in the South American clade of fire ants, but not in the related *S. geminata*.

Queen number may greatly influence intraspecific recognition in social insects, because the presence of multiple queens in a colony can increase the number of genetically based cues used to create the template an individual uses for perception. Subsequently, increasing queen number may diminish the accuracy of nestmate recognition systems (Hölldobler & Wilson 1977, Stuart 1991, Starks *et al.* 1998). There is some evidence that nestmate discrimination among workers is relaxed in multiple queen (polygynous) colonies of fire ants (Morel *et al.* 1990) relative to single queened (monogynous) colonies (Adams & Tschinkel 2001). Given that polygyne colonies occur at greater densities than monogyne colonies in introduced populations of fire ants (Macom & Porter 1996), and appear to have greater impacts on native species (Porter & Savignano 1990), the link between variation in nestmate discrimination and invasion success warrants further investigation.

Formosan termites

Native to China, Formosan termites (*Coptotermes formosanus*) have invaded South Africa, North America, the Hawaiian Islands, Japan, the Philippines and Taiwan (reviewed in Wang *et al.* 2002). In Hawaii, this species shows some intercolonial aggression (Su & Haverty 1991), although levels of intraspecific aggression are reduced relative to other termites (Husseneder & Grace 2001a). In Florida, however, intraspecific aggression is apparently entirely absent (Su & Haverty 1991). Interestingly, several colonies from Florida and Hawaii did not show aggression towards each other, even though they may not be from the same introduction event. Colonies from Florida and Hawaii can be reliably distinguished based on their cuticular hydrocarbon profiles, but differences in cuticular hydrocarbon profiles did not correlate with levels of aggression between colonies (Su & Haverty 1991).

Individual colonies in Hawaii can be distinguished by their cuticular hydrocarbon profiles (Haverty *et al.* 1996). These colonies are genetically distinct and moderately inbred, and there are relatively high levels of genetic diversity within the population (Husseneder & Grace 2001b). However, a comparison of behavioral and genetic patterns between native and introduced populations is still necessary to determine if the invasion process has changed the recognition system of *C. formosanus*.

These patterns suggest that despite substantial genetic diversity (Husseneder & Grace 2001a) and variation in chemical and environmental cues (Haverty *et al.* 1996), nestmate recognition is not always seen. It is possible that discrimination still occurs but resulting actions by recipient termites do not include aggression (Thorne & Haverty 1991). This may result if the costs of aggression are sufficiently high, perhaps due to increased encounters among non-nestmates resulting from high densities in introduced populations (Giraud *et al.* 2002). Alternatively, there may be a shift in the signals given by individuals such that all individuals meet the nestmate acceptance threshold (Starks 2003).

Many invasive species are social or at least gregarious (Ehrlich 1989, Lodge 1993), a behavior mediated by a highly tuned recognition system. It is unclear how the invasion process might affect social interactions among species generally, but insights from social insects suggest that both founder events and selection may reduce levels of intraspecific aggression in introduced populations relative to native populations. Whether this phenomenon extends to other social insect invaders, many of which are unicolonial (Passera 1994, Holway *et al.* 2002), or to other invasive organisms, warrants further investigation.

Interspecific recognition: predation

The evolutionary arms race between predators and prey has led to myriad ways in which prey species protect themselves against predation, including morphological, physiological, and behavioral adaptations (reviewed in Endler 1991). Morphological adaptations can include specialized spines, hairs, and coloration such as startling patterns (e.g. eye spots) or crypsis. Some prey species synthesize or sequester noxious or toxic chemicals that afford them protection and these species often display aposematic coloration (Roth & Eisner 1962, Nishida 2002). Predators can have a learned or innate ability to recognize these bright colors, and avoid them. Classic studies of scrub jays (*Cyanocitta coerulescens*) (Brower 1958) and blue jays (*Cyanocitta cristata*) (Brower 1969, Platt *et al.* 1971) are examples of a predator learning to recognize and avoid unpalatable prey. Jays lacking prior experience with monarch butterflies (*Danaus plexippus*) will eat them the first time they are encountered and vomit soon thereafter; jays will not repeat an attempt to eat another monarch (or similarly colored butterfly). Innate (heritable) avoidance of warning coloration has also been demonstrated in many species of birds (Smith 1975, 1977, Lindström *et al.* 1999).

Behavioral responses to the threat of predation require that prey species recognize cues produced by their predators. Some animals not only differentiate between cues produced by different predators, but also may have species-specific responses. For example, some noctuid moths avoid bat predation by detecting their ultrasonic calls and subsequently changing their flight pattern (Roeder 1966). Vervet monkeys (*Cercopithecus aethiops*) and suricates (*Suricata suricatta*), have predator specific alarm calls that initiate different defensive behaviors according to the type of threat (Seyfarth *et al.* 1980, Manser 2001, Manser *et al.* 2002). Animals that rely on recognition cues to mount a behavioral anti-predator response may be especially susceptible to the introduction of novel predators.

Predator recognition systems may be general or specific. General predator recognition systems should work effectively under a variety of different conditions, but recognition of specific predators often involves experience, learning, or a long co-evolutionary history between predator and prey. Consequently, recognition systems for particular predators leave prey vulnerable when they encounter a novel predator. Thus, general predator recognition systems appear effective against newly introduced predators, but species that rely upon specific systems may experience a lag period between the introduction of the predator and the acquisition of anti-predator responses.

Plasticity and learning are extremely important characteristics for both introduced predators and their potential prey. In the context of biological invasions, appropriate reactions are elicited from animals only if their template expands to include signals produced by novel prey or enemies. Naïve prey that fail to recognize a new threat will be ill-equipped to defend against a novel predator (with which they have no experience or evolutionary history), and may eventually go extinct, as seen in many island systems (Steadman 1995, Fritts & Rodda 1998). However, several examples demonstrate that species can respond to novel predators or prey either through learned or innate mechanisms.

Learned recognition of novel predators

New Zealand robins provide an example of how recognition systems can adapt to the introduction of a novel predator. Maloney and McLean (1995) tested the response of predator-experienced robins from the mainland and naïve robins from a small island (where mammalian predators are absent) to a model of an introduced nest predator (the stoat, *Mustela erminea*) and a control (a cardboard box of similar size) positioned near the nest during breeding season. Experienced birds exhibited increased alarm behaviors when the stoat was present, including wing flicking and drooping, alarm calls, and head feather displays; experienced birds did not respond to the control box. Naïve birds showed similarly low levels of alarm to both the model predator and the control. In a second experiment, Maloney and McLean (1995) trained naïve robins to respond to the predator by associating the presence of the model stoat with robin alarm and distress calls, and a model robin in a mobbing posture. Naïve birds witnessing these stimuli increased their alarm behavior towards the model stoats. In this example, learning is part of the predator recognition system in New Zealand robins. An important conservation implication highlighted by Maloney and McLean (1995) is that captive breeding and reintroduction programs could be facilitated by training endangered species to recognize their predators.

Innate recognition of novel predators

In the Pacific Northwest of the United States, Pearl *et al.* (2003) found evidence for innate recognition of introduced predators in one of two native frog species. Larvae of the Pacific treefrog (*Pseudacris regilla,* formerly *Hyla regilla*) and the red-legged frog (*Rana aurora*) responded to cues of redside shiners (*Richardsonius balteatus*), a native predator, by spending a larger proportion of their time in a refuge. However, only *R. aurora* responded to waterborne cues of introduced predators such as bluegill sunfish (*Lepomis macrochirus*) and crayfish (*Procambarus clarkii*). These data suggest that *R. aurora* might have a broader template for predator recognition than *P. regilla* and therefore be more resistant to predation pressure from introduced predators.

Pearl and colleagues also found the introduced bullfrog (*Rana catesbeiana*) exhibited increased refuge use when its water was conditioned with the scent of predators from outside its native range, but not when presented with cues of predators from within its native range that find bullfrogs unpalatable. The ability of bullfrog larvae to recognize cues of novel predators that may find them palatable can contribute to their success as an invasive species (Pearl *et al.* 2003).

Interestingly, Pacific treefrog juveniles and red-legged frog larvae have developed the ability to recognize bullfrogs since this predator's introduction to the western United States approximately 70 years ago. Populations of *R. aurora* and *P. regilla* sympatric with the invasive bullfrog avoid chemical cues of the bullfrog while frogs from populations allopatric with bullfrogs do not avoid the scent of this predator (Kiesecker & Blaustein 1997, Chivers *et al.* 2001). These differences in response to predator cues between sympatric and allopatric populations of *R. aurora* result in the higher avoidance of predation by the sympatric populations, indicating that failure to recognize a predator's odor and to behave appropriately has severe negative fitness consequences. However, larval *R. aurora* that reduced their activity and increased refuge use had slower growth and smaller metamorphosis weight (Kiesecker & Blaustein 1998), suggesting that avoiding predation by introduced bullfrogs is not without some cost. Both studies (Kiesecker & Blaustein 1997, Chivers *et al.* 2001) suggest that the predator recognition profiles of the native *P. regilla* and *R. aurora* are plastic and can shift to incorporate new predators in a relatively short period of time.

Kiesecker and Blaustein (1997) reared the larvae in their experiments from eggs. The larvae from the different populations therefore had no prior experience with bullfrog predators, yet the differences in response to bullfrog cues persisted. This suggests a possible genetic component to the recognition of this predator's cues. The extent to which environment and genes interact to result in the behavioral differences between the populations of *R. aurora* is an open question. Future work should focus on the heritability of recognition of novel predator cues in this and other systems. Understanding how the environment and genes affect different prey species' response to novel predator cues could lead to insights about why some species are capable of adjusting to the presence of novel predators, yet other prey organisms cannot.

Interspecific recognition: parasitism

Like predator-prey systems, host-parasite interactions can be highly co-evolved, and parasites are often invoked as an important driving force behind population dynamics (Dobson & Hudson 1986, Price *et al*. 1986). In the context of biological invasions, a lack of parasites and pathogens in an invader's introduced range is one of the leading hypotheses for the success of invasive species (Keane & Crawley 2002, but *see* Colautti *et al*. 2004).

Coevolution between host and parasite can result in dynamic, highly tuned recognition systems. Selection can refine the template hosts use to detect parasites, while honing the signals parasites use to exploit their hosts. When a parasite is introduced to a new range or host, this finely tuned balance of signals may be upset. Recognizing new signals and adjusting templates to account for novel hosts is crucial for invasive parasites. It is equally important for novel hosts to recognize new parasites to mount an effective defense.

Brown-headed cowbirds

The brown-headed cowbird (*Molothrus ater*) is an obligate brood parasite that is known to parasitize over 200 species in North America (Rothstein 1990). Although native to North America, cowbirds are currently expanding their range along the west coast and in Florida (Rothstein 1994, Cruz *et al*. 2000). This invasion provides an opportunity to study both the mechanisms involved in the exploitation of novel hosts by *M. ater* and the ability of naïve hosts to recognize signals of parasitism (the presence of adult cowbirds or foreign eggs). Cowbirds are contributing to the decline of many species of songbirds in North America (Robinson *et al*. 1995), whose persistence may depend on the development of appropriate responses to brood parasitism. These responses include foreign egg recognition and rejection, nest abandonment, or reduced clutch size (Rothstein 1990, Hauber 2003, Goth & Hauber 2004).

Varroa mites

The *Varroa* mite (*Varroa jacobsoni*, formerly *V. destructor*), a parasite of the Indian honeybee (*Apis cerrana*), began parasitizing the European honeybee (*Apis mellifera mellifera*) in 1905 (reviewed in Oldroyd 1999). The mite subsequently spread throughout the European honeybee's range, posing a serious threat to the world's apiculture industry. Female mites lay eggs on the walls of brood cells prior to capping by nurse bees. Concurrent with a shift in host species, female mites changed their oviposition behavior; while *V. jacobsoni* parasitizes male brood almost exclusively when associated with *A. cerrana*, it will parasitize both male and worker brood in *A. mellifera*. This host shift has been accompanied by a change in the template of female mites — the signals provided by worker brood are different than male brood (Le Conte *et al*. 1989), and the mites have had to develop the ability to recognize novel oviposition sites. In some cases, *V. jacobsoni* females are unable to oviposit on *A. mellifera* because of a lack of an appropriate signal (Martin *et al*. 1997).

Varroa jacobsoni have different success rates among races of *Apis mellifera* (Guzman-Novoa *et al*. 1996; Aumier *et al*. 2002). Africanized honeybees (*Apis mellifera scutellata*) are resilient to *V. jacobsoni* infestations because they have a defense known as hygienic behavior (Spivak 1996). In apiary conditions, European honeybees are infected at higher rates than Africanized honeybees (Aumier *et al*. 2002). In this case, the template of the host shifted, so that Africanized honeybee workers recognize novel signals from *V. jacobsoni* and eliminate infected brood. The change in cuticular hydrocarbon (CHC) profile of an infected host may be very subtle; there was no qualitative difference in the CHC profiles of three stages of infested or uninfested bees, although proportions of CHCs changed according to severity of infection (Salvy *et al*. 2001).

In the short amount of time *Varroa jacobsoni* has been associated with *Apis mellifera*, the mite has been able to develop chemical mimicry of its host (Martin *et al*. 2001). The CHC profile of *A. mellifera* changes as it matures (Trouiller *et al*. 1991, Aumier *et al*. 2002), and *V. jacobsoni* may recognize honeybee larvae of different stages by their different relative proportions of CHCs (Rickli *et al*. 1994). The CHC profiles of mites in cells change in a manner that tracks the shift in their host's signature (Martin *et al*. 2001). This reduces the chance of being eliminated by hygienic behavior of *A. mellifera* workers. It is not clear whether the shift in the mite's CHC profile is caused by absorption of molecules from the hemolymph of the host, contact with host materials, or by active metabolism (Katase & Chino 1982, Martin *et al*. 2002), but attaining the signature of the host is key to prolonged breeding in the host colony.

Both *V. jacobsoni* and *A. mellifera* are experiencing challenges to their recognition systems as a result of the host shift and range expansion of *V. jacobsoni*. The economic impact of this invasion may ultimately be determined by the ability of honeybees to recognize new signals and change their behavior. *Varroa jacobsoni* has already demonstrated the ability to adapt to the signals of a novel host, and has changed the template used to assess whether a host is suitable. Without proper host recognition, *V. jacobsoni* would not have been able to invade successfully. Similarly, selection should favor a modification of *Apis mellifera's* template to recognize and eliminate infected brood. The higher rates of rejection behavior in Africanized honeybees may be related to high levels of parasitism in the environment in which they evolved. For example, the aggressive nature of Africanized honeybees has been attributed to the high threat of predation in their native range (Winston 1987), and increased vigilance against parasites may have evolved in a similar manner. It would be worth investigating if there is a link between increased aggression and increased ability to recognize infected brood.

Conclusions and future directions

The biological processes associated with invasions can modify recognition systems at multiple levels, including recognition of self, recognition of conspecifics, and recognition of heterospecifics including predators and prey, parasites and hosts. Below we summarize some important avenues for future research.

Recognition systems may be particularly sensitive to reductions in population size. Propagules of invading species may be small and newly established populations often undergo severe bottlenecks potentially causing both genetic and demographic problems. Individuals will subsequently have a hard time locating appropriate mates and selection may relax the stringency of what is acceptable. Rapid population level genetic changes during introduction can also result in pronounced differences in the diversity and frequency of alleles used in allorecognition systems, leading to changes in behavior between native and introduced populations. To fully understand how recognition systems are influenced by these demographic and genetic factors, it is imperative to compare successful with unsuccessful invasions. However, it is notoriously difficult to collect data on failed invasions.

In addition to demographic and genetic factors, introduced species will encounter and need to interpret novel abiotic and biotic stimuli. Finding appropriate habitat and food is crucial for the survival of an invader. Learning to recognize new signals, and plasticity in the template used to assess what is an acceptable resource, can be key to the success of invasive species. The introduction of novel predators also provides an opportunity to understand the importance of innate and learned cues for recognition. Several examples demonstrated flexibility in recognition systems, both in invasive species and in species with which they interact. It remains an open question whether plasticity in recognition systems makes an organism a better invader or if the invasion process selects for increased flexibility. Examining the influence of biological invasions on recognition systems will yield insights about the evolution/adaptation of recognition systems as organisms either learn new cues, or populations adapt to new environments. Conversely, a careful understanding of the recognition systems of invaders may provide insight into the success of some species.

Ultimately, questions about the impact of invasions on recognition systems necessitate a comparative approach between native and introduced populations. The behavior or population structure of invasive species in their native range should be the standard to which invasive populations are compared. Studying an introduced population in isolation can yield misleading results. Independent introduction events of invasive species from their native range, or from other introduced populations, also represent a natural experiment for understanding the influence of genetic and environmental variation on recognition systems.

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