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The Neuroecology of Competitor Recognition

Permalink

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Journal

Integrative and Comparative Biology, 51(5)

ISSN

1540-7063 1557-7023

Author

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Publication Date

2011-06-22

DOI

10.1093/icb/icr060

Peer reviewed



SYMPOSIUM

The Neuroecology of Competitor Recognition

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From the symposium “Neuroecology: Neural Determinants of Ecological Processes from Individuals to Ecosystems” presented at the annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2011, at Salt Lake City, Utah.

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Synopsis Territorial animals can be expected to distinguish among the types of competitors and noncompetitors that they encounter on a regular basis, including prospective mates and rivals of their own species, but they may not correctly classify individuals of other species. Closely related species often have similar phenotypes and this can cause confusion when formerly allopatric populations first come into contact. Errors in recognizing competitors can have important ecological and evolutionary effects. I review what is known about the mechanisms of competitor recognition in animals generally, focusing on cases in which the targets of recognition include other species. Case studies include damselflies, ants, skinks, salamanders, reef fishes, and birds. In general, recognition systems consist of a phenotypic cue (e.g., chemical, color, song), a neural template against which cues are compared, a motor response (e.g., aggression), and sensory integration circuits for context dependency of the response (if any). Little is known about how competitor recognition systems work at the neural level, but inferences about specificity of cues and about sensory integration can be drawn from the responses of territory residents to simulated intruders. Competitor recognition often involves multiple cues in the same, or different, sensory modalities. The same cues and templates are often, but not always, used for intraspecific and interspecific recognition. Experiments have shown that imprinting on local cues is common, which may enable templates to track evolved changes in cues automatically. The dependence of aggression and tolerance on context is important even in the simplest systems. Species in which mechanisms of competitor recognition are best known offer untapped opportunities to examine how competitor-recognition systems evolve (e.g., by comparing allopatric and sympatric populations). Cues that are gene products (peptides, proteins) may provide insights into rates of evolution. There are many avenues for further research on the important but understudied question of how animals recognize competitors.

Introduction

Competitor recognition can be defined as the process of identifying, and of discriminating among, different classes of competitors and noncompetitors (Grether et al. 2009). Its adaptive value is most easily seen in territorial species. Residents of a territory must decide how to respond to intruders. Some intruders represent a competitive threat while others represent no threat, or even possible opportunities for mating. Failing to evict competitors for resources is costly, but so is evicting potential mates and noncompetitors. Thus, we can expect territorial animals to have well-developed mechanisms for distinguishing among the types of competitors and noncompetitors that they are likely to encounter on a regular basis, and this would at least include

prospective mates and rivals of their own species. On the other hand, animals cannot be expected to correctly classify individuals of other species that they rarely, if ever, encounter.

Closely related species often have similar phenotypes and this can lead to confusion when formerly allopatric species first come into contact (i.e., secondary contact). Errors in recognizing competitors can have important ecological and evolutionary effects (Grether et al. 2009). Aggression between species may cause competitive exclusion of rare or behaviorally subordinate species, even in the absence of interspecific competition for resources (Case and Gilpin 1974). If the species manage to coexist, selection against interspecific aggression may cause the competitor-recognition systems of the species to

diverge from each other (Lorenz 1962, 1966). Conversely, if the species are in competition for limiting resources, selection may favor convergence in their competitor-recognition systems (Cody 1969, 1973).

A general term for evolutionary responses to aggression between species is agonistic character displacement (ACD). ACD is directly analogous to reproductive character displacement and affects some of the same traits, but the mechanisms of selection and the range of possible evolutionary outcomes are different (Grether et al. 2009). A recent review of the literature suggests that ACD is likely to be prevalent in a variety of taxa and systems (Grether et al. 2009). Taxonomically, the list of putative cases includes insects, fishes, amphibians, lizards, bats, and birds. While most cases involve shifts in the phenotypic cues that animals use to recognize competitors, other cases involve shifts in how animals respond to heterospecifics without corresponding shifts in agonistic cues. For example, common chaffinches (*Fringilla coelebs*) and blue chaffinches (*Fringilla teydea*) respond less aggressively to each other's songs in areas of sympatry than they do in areas of allopatry, which may enable the species to coexist without defending interspecific territories (Lynch and Baker 1991).

Prevalence of interspecific aggression

According to recent meta-analyses, aggression between species is extremely common and often just as intense as intraspecific aggression (Ord and Stamps 2009; Peiman and Robinson 2010; Ord et al. 2011). In some cases, interspecific aggression occurs at rather high rates even though the species do not appear to be in competition for limiting resources. Why do such cases of "misdirected aggression" persist? What prevents the species from diverging in competitor recognition?

Rubyspot damselflies (genus *Hetaerina*) are an example of a taxon in which aggression between sympatric species appears to result from errors in competitor recognition (Johnson 1963; Anderson and Grether 2011). Only mature males are territorial and they are only territorial at the times and places at which females oviposit. Feeding occurs elsewhere and males do not defend access to oviposition substrate. The primary benefit of territoriality in this system is that resident males have priority of access to arriving conspecific females (Weichsel 1987) and there is no obvious benefit to excluding heterospecific males (Anderson and Grether 2010b). Yet some *Hetaerina* species-pairs are interspecifically territorial (Anderson and Grether 2011). Within species,

competitor recognition in *Hetaerina* appears to be based on wing coloration. Mature males of all *Hetaerina* species have red spots at the base of their wings; these spots are absent on females and immature males (Garrison 1990) (Fig. 1A). Experiments using tethered intruders and wing-color manipulations (Fig. 1B) have shown that the competitor recognition systems of some, but not all, species pairs have diverged from each other in sympatry (Fig. 1C and D) (Anderson and Grether 2010a, 2010b). What accounts for the lack of divergence in some species-pairs? We are investigating selection-based explanations (e.g., Anderson and Grether 2011), but perhaps the lack of divergence simply reflects constraints on what damselfly brains are able to distinguish. Selection requires variation, and some minimal level of divergence in coloration before secondary contact may be required for sympatric species to diverge in their recognition competitor systems.

Goals of this article

The main goal of this article is to review what is known about the mechanisms of competitor recognition in animals generally and to consider how these mechanisms might affect evolutionary responses to aggressive interference between species. First, I outline the general components of recognition systems and the first layer of questions that need to be asked about the mechanisms of competitor recognition. In the body of the article, I review what is known about competitor recognition systems of some selected taxa, focusing on cases in which it is known that the targets of recognition include other species. Finally, I summarize what we have learned and identify promising directions for further research.

General components of recognition systems

Recognition systems in general include at least three components: an expression component consisting of a phenotypic cue (or label) expressed by the target individual, a perception component, consisting of a neural template in the other individual (actor) against which the cue is compared, and an action component, i.e., the behavioral response of the actor to the target (Tsutsui 2004; Newey et al. 2010). Possible cues include volatile chemicals, cell-surface proteins, songs, color patterns, behavioral patterns, i.e., any detectable phenotypic trait. In the case of competitor recognition, the relevant phenotypic cues are often secondary sexual traits with age-limited and/or sex-limited expression. Another

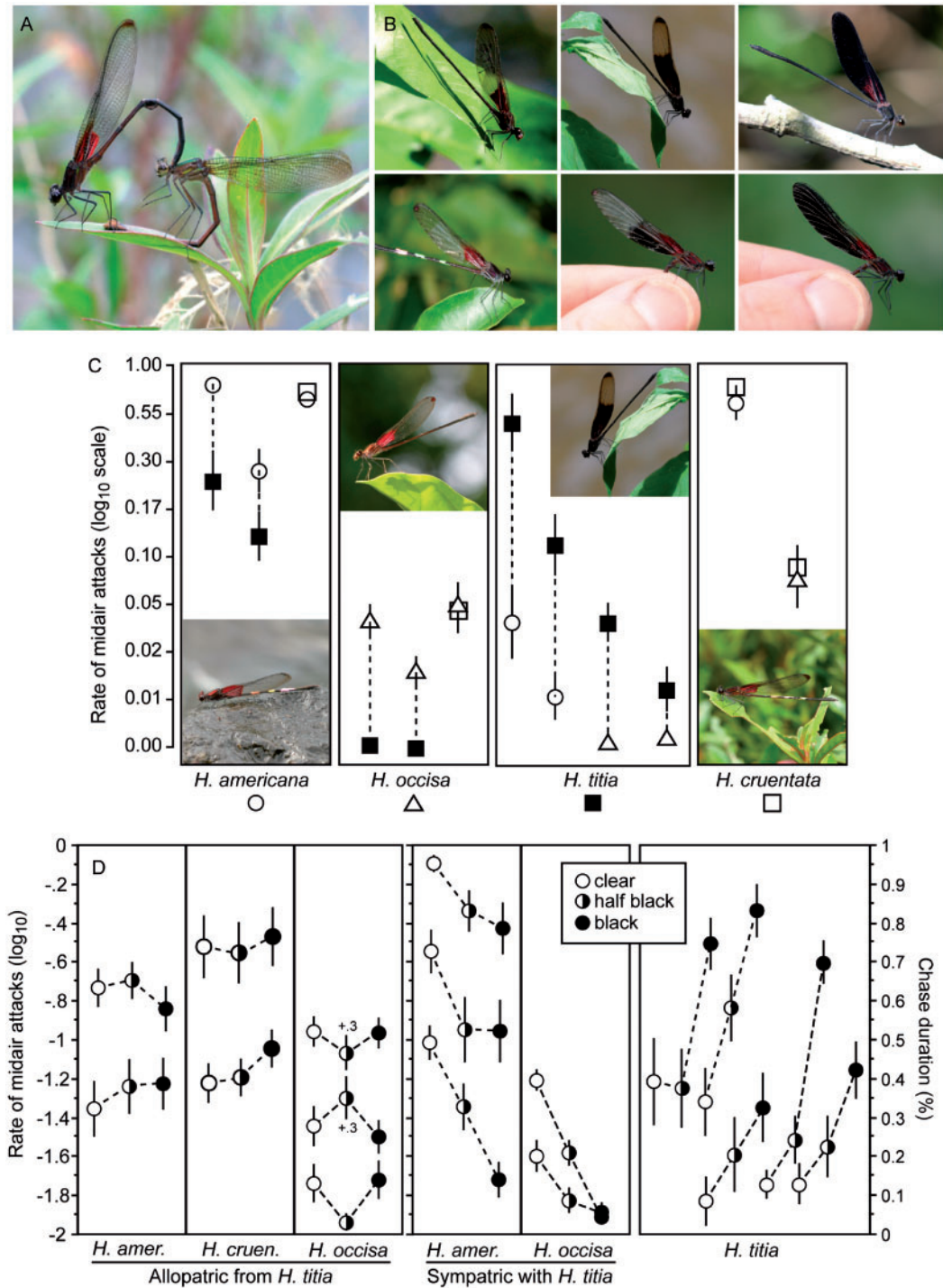


Fig. 1 (A) Mating pair of *Hetaerina cruentata* (male on left, female on right). (B) Range of variation in wing coloration of male *Hetaerina titia* in Mexico (upper three panels); male *Hetaerina occisa* with experimentally altered wing coloration (lower three panels; see below). (C) Responses of territory holders of four *Hetaerina* spp. (named below graphs and shown in photos) to tethered conspecifics and sympatric congeners. Symbols identify the species of the intruders (see symbol key below graph). Vertical dashed lines connect means (\pm SE) for tests carried out at the same site. Overlapping points are not significantly different; for all others $P < 0.05$. Note lack of discrimination between species that are similar in coloration. (D) Evidence for enhanced competitor recognition in sympatry. Summary of results from multiple sites where territory holders were presented with tethered *Hetaerina americana* or *H. occisa* intruders (dashed lines connect means \pm SE for the same site). Tethered males were given one of the three wing-color treatments shown in (B): clear, half black/half clear, or black. Adding black to the wings increases the resemblance to *H. titia* [see (B)]. The graphs show that blackening tethered intruders' wings increased aggression from *H. titia* territory holders (right panel), reduced aggression from *H. occisa* and *H. americana* territory holders in sympatry with *H. titia* (middle panel), and had no significant effect on aggression from *H. occisa*, *H. americana* or *H. cruentata* in allopatry (left panel). The effect of sympatry with *H. titia*, as measured by the treatment by site–category interaction, was highly significant for both *H. occisa* and *H. americana* ($P < 0.001$). Figures redrawn using data published by Anderson and Grether (2010b).

Table 1 General components of recognition systems

Component	Description
Expression component	phenotypic cue (or label) expressed by the target individual
Perceptual component	neural template in the other individual (actor) against which the cue is compared
Motivational component	neural circuitry responsible for context-dependence of the behavioral response
Action component	behavioral response of the actor to the target

common, if not universal, feature of competitor-recognition systems is context dependence: actors only distinguish between target cues in certain contexts. For example, male *Hetaerina* damselflies only react aggressively to conspecific males at the times when, and locations where, females are likely to oviposit (Weichsel 1987; Grether 1996). Thus, while finding a differential response to individuals with different cues is sufficient to conclude that perceptual discrimination has occurred, the lack of a differential response might only reflect a lack of motivation to respond differently toward individuals with different cues (Newey et al. 2010). As the link between perception and action, motivation is an integral component of most recognition systems (Table 1).

Questions about competitor-recognition mechanisms

To my knowledge, no competitor-recognition templates have yet been fully characterized at the neural level. Even in the best-studied systems, what we know about the perception component of recognition is mainly based on behavioral responses of animals to cues. Nevertheless, many useful inferences about the mechanisms of competitor recognition can be made at this level. Here is a partial list of the sort of questions that need to be asked about competitor-recognition templates:

(1) How specific is the neural template? For example, if the phenotypic cue is a color mark, does the brightness, size, placement, or number of such marks matter or does the template only recognize presence versus absence? This is relevant to understanding the possible evolutionary responses to secondary contact between species that still share very similar competitor-recognition systems. Suppose selection favors reduced interspecific aggression. If competitor recognition is based on the simple presence or absence of an age/sex-specific cue, and the two species have the same age/sex-specific cue, then no simple mutation in the cue or template would increase in frequency due to selection.

If, instead, activation of the template depends on variable properties of the cue (e.g., size, location) then any initial difference between the templates of the two species could facilitate further divergence in cue and/or template.

- (2) Does the neural template integrate input from multiple sensory modalities (e.g., sight, sound, smell) or multiple types of input from a single sensory modality (e.g., patterns of motion and color pattern; volatile and nonvolatile chemical cues)? If multiple cues are used, how are they weighted in the nervous system? Is the information provided by different cues merely redundant or are different cues used at different distances or in different contexts? If recognition is based on multiple cues, this might facilitate divergence, simply because there are more ways for species to diverge.
- (3) How is activation of the template linked to the motor response? Is aggression released by the presence of a competitor's cue or the absence of a noncompetitor's cue, or both? For example, do territorial males detect male intruders based on the presence of cues to maleness, the absence of cues to femaleness, or both? and
- (4) Are templates "hardwired" or formed/modified by experience? If the latter, what experiences are required for normal formation of the template? What are the developmental mechanisms: imprinting during a critical period, habituation, trial-and-error individual learning, or social learning? Have the mechanisms for template formation/modification themselves evolved in an interspecific context? This could be investigated by examining whether sympatric populations are better than allopatric populations at learning to distinguish between conspecifics and heterospecifics.

Competitor-recognition systems in diverse taxa

I carried out a literature review with the above questions in mind to find out what is known about the

mechanisms of competitor recognition in animals generally. What follows is far from comprehensive but is meant to characterize the state of knowledge of the mechanisms of competitor recognition in some well-studied systems.

Ants

Ants distinguish between nestmates and members of other colonies and species based on chemical cues, including airborne chemicals as well as nonvolatile cuticular hydrocarbons (CHCs). The CHC profile of an ant colony is a moving target, in part because diet affects CHCs and food sources change over time. The recognition system of ants must therefore allow them to adjust to changes in the CHC profile of their own colony while retaining the ability to recognize foreign intruders (Leonhardt et al. 2007). Ants typically are aggressive to other colonies of the same species and to other species that are in competition for common resources. At a minimum, this requires workers to distinguish among colony mates, conspecifics from other colonies, heterospecific competitors, and heterospecific noncompetitors.

The details of how the recognition system works depend on the species. Individuals may only learn to recognize self-cues or they may learn to recognize cues present on colony mates that they do not themselves express. Some responses to heterospecifics may be innate, but it is known in some cases that tolerance of heterospecifics is acquired and involves some of the same mechanisms as the development of tolerance toward same-colony conspecifics (reviewed in Errard et al. 2008). Newly emerged (callow) ants often lack colony-specific CHCs and can be transplanted between colonies without being attacked. Over the first few hours of adult life, callow ants may imprint on the CHC profile of their colony and acquire the colony-specific CHCs. This generally requires direct interactions with nestmates, including antennation, allogrooming, and trophallaxis, although it has also been shown that ants can imprint on volatile chemical cues (Errard et al. 2008). This learning process not only enables ants to distinguish between colony mates and conspecific ants from other colonies but also to distinguish between colonies of other species. This has been shown experimentally, with artificial mixed-species associations, and also under natural conditions in parabiotic associations in which two species of ants use the same nest and the same chemical trails (Orivel et al. 1997; Errard et al. 2003). In such associations, workers tolerate nestmates of both species and are aggressive to intruders from other colonies of both species. This

requires workers to learn two different colony CHC profiles, because the colonies in a parabiotic association retain distinctly different CHC profiles (Errard et al. 2008).

While it is clear that ants use chemical cues to discriminate between nestmates and intruders, exactly how they do so is incompletely understood. Under the prevailing *Gestalt* colony odor model, ants distinguish between nestmates and nonnestmates by comparing the entire chemical profile of an encountered individual to a representation of a colony odor stored in a neural template (reviewed in Guerrieri et al. 2009). Based on this model, ants defending their nest would be expected to respond aggressively to intruders that either lacked a familiar chemical cue or presented an unfamiliar chemical cue. To test this prediction, Guerrieri et al. (2009) manipulated the CHC profile of carpenter ants by adding synthetic hydrocarbons to their food. They found that the presence of a new hydrocarbon was sufficient to elicit aggression from subcolonies that did not receive the food supplement, but subcolonies that received the food supplement were not aggressive to ants that lacked the new hydrocarbon. Based on these results, Guerrieri et al. (2009) proposed that the recognition system of ants only detects unfamiliar chemical cues and does not respond to the absence of familiar chemical cues. Whether this alternative model applies to other species of ants (or even to carpenter ants under all circumstances) remains to be determined, but the experimental approach taken by Guerrieri et al. (2009) seems promising.

Other insights about the recognition system of carpenter ants can be gleaned from Guerrieri et al.'s (2009) experiment. Although adding synthetic hydrocarbons to the food supply changed the CHC profile of a subcolony in <24 h, this did not lead to increased levels of aggression within the group. Apparently, the neural template that carpenter ants use for recognizing nonnestmates is updated rapidly as the colony's hydrocarbon profile changes (see Leonhardt et al. 2007). The experiment by Guerrieri et al. (2009) also revealed constraints on the flexibility of the recognition system: of three synthetic hydrocarbons tested, only one elicited aggression from subcolonies that had not been exposed to the same compound.

What is actually happening at the neural level? Adaptation at the level of antennal receptors is the simplest possible explanation (Ozaki et al. 2005), but this appears to have been ruled out. It takes hours, not minutes, for carpenter ants to stop being aggressive to nonnestmates after the chemical cues of

nonnestmates are applied directly to their antennae (Leonhardt et al. 2007). This suggests a learning process (habituation) at least at the level of the antennal lobes (the first area to process olfactory input) if not deeper in the brain (Guerrieri et al. 2009).

While habituation at a middle sensory-processing level might account for the perceptual component of the ant's recognition system, some higher level of sensory integration must also be involved. Tanner et al. (2006, 2008, 2009) have studied the context dependence of aggression by the wood ant *Formica xerophila* toward a behaviorally dominant congener with which it competes for access to common resources (*Formica intergroides*). In some experiments, the behavior of the congener was ruled out as a contributing factor through the use of artificial ants (glass beads coated with ants' surface lipids). Factors that have been shown to modulate the aggressive response of *F. xerophila* include group size and location. *Formica xerophila* were less likely to retreat and more likely to attack when present in larger numbers, and they were more aggressive to the other species while defending their nest than while defending food. Furthermore, while defending food, *F. xerophila* were less aggressive to *F. intergroides* from neighboring colonies than to *F. intergroides* from distant colonies, but this "dear enemy" effect was not seen in workers defending the nest. While these results are not surprising from a functional standpoint, they illustrate that responses to the same competitor's cues can vary depending on the context of the encounter. Thus, even in animals as simple as individual worker ants, the motivational component of recognition needs to be taken into account.

Skinks

Skinks in the genus *Eumeces* provide an example of a system in which competitor recognition is based on a combination of visual and olfactory cues. Three species can be found both in allopatry and in sympatry with each other in the eastern United States (Cooper and Vitt 1987). Morphologically and ecologically, these species are very similar, so much so that they were originally classified as one species (Taylor 1935). All three species are active at the same times of day, forage in similar places (trees and surface litter), and breed at the same times of year (Cooper and Vitt 1987). Adult males fight frequently during the breeding season but only with other adult males of the same species (Vitt and Cooper 1985). Thus, while these species may be ecological competitors, aggression appears to be used only for

competition for mates within species. Through a series of staged encounters and manipulations of phenotype, Cooper and Vitt (1987, 1988) showed that adult males initially distinguish males that are potential competitors from females and from immature males using visual cues that are specific to adult males but do not differ between the species (color and shape of the head). At closer range, males distinguish between adult males of their own species and those of other species using chemical cues. Males tongue-flick each other (chemosensory behavior) prior to fighting and ordinarily will break off interspecific interactions at this stage. That chemical cues are responsible for discrimination at this stage was confirmed by transferring cloacal chemicals between species (Cooper and Vitt 1987). Olfactory discrimination probably occurs in the vomeronasal organ (VNO) (Cooper 1994). The role of head coloration at the initial stage of an encounter was demonstrated by painting females' heads orange like those of mature males (Cooper and Vitt 1988). Males initially responded aggressively to orange-headed females, but then ceased being aggressive after tongue-flicking the female's body or the substrate where she had walked. Thus, chemical cues appear to take precedence over visual cues in recognition of competitors both within and between species. Cooper and Vitt (1987) hypothesize that species-identifying pheromones of males evolved in response to selection against interspecific aggression (the pheromones themselves have not been identified).

Salamanders

Salamanders also use both vision and olfaction to detect intruders (Page and Jaeger 2004; Kohn and Jaeger 2009) but probably rely more on olfaction than do skinks. Red-backed salamanders (*Plethodon cinereus*) can detect intruders based on both nonvolatile and volatile pheromones deposited on the substrate (Martin et al. 2005; Dantzer and Jaeger 2007). Adults of both sexes are territorial (Mathis 1991; Gillette et al. 2000) and respond more aggressively to the scent of intruders of their own sex (Dantzer and Jaeger 2007). The primary scent-marking pheromones of this species are produced by a gland posterior to the cloaca (Simons et al. 1994). Pheromones are detected through a stereotypical behavior (nose tapping) that puts the nasolabial cirri into contact with the substrate and allows nonvolatile chemicals to move up into the VNO (Dawley and Bass 1988, 1989). Volatile pheromones are presumed to be detected by the main olfactory system (reviewed in Dantzer and Jaeger 2007). Besides identifying an

individual's sex, the postcloacal pheromones have been shown to allow individuals to recognize each other uniquely and to convey aspects of individual competitive ability (Simons et al. 1997; Wise et al. 2004; Martin et al. 2005). Male red-backed salamanders have been shown to prefer the airborne chemical cues of conspecific females over those of heterospecific females (Dawley 1984). Thus, it seems likely that salamanders could use chemical cues to discriminate between conspecific and heterospecific intruders in a territorial context.

Some sympatric *Plethodon* species interact aggressively with each other and the intensity of interspecific aggression varies geographically (reviewed in Hairston 1983; Nishikawa 1987; Ransom and Jaeger 2006; Grether et al. 2009). Whether the variability in interspecific aggression reflects varying degrees of divergence in pheromone-based competitor recognition is unknown but could be tested by experiments in which salamanders are presented with conspecific and heterospecific chemical cues (see Dawley 1984).

Most research on *Plethodon* pheromones has focused on male–female interactions (reviewed in Woodley 2010). The advances that have been made in this area point to promising directions for research on pheromones used in competitive interactions. Male red-legged salamanders (*Plethodon shermani*) deposit secretions of the mental gland directly on females during courtship and, based on the location of the gland, they might also use these secretions for marking the substrate (Schubert et al. 2009). The overall effect of the pheromones deposited on females is an increase in the female's receptivity and a reduction in the length of some stages of the courtship sequence (Rollmann et al. 1999; Houck et al. 2007). Thus far, three mental-gland proteins have been isolated and shown to alter females' behavior. Woodley (2010) described in detail how these putative pheromones were identified, screened for their effects on females' behavior, and characterized biochemically. Interestingly, each of these chemicals has different effects on females' behavior, and one had the unexpected effect of slowing down certain stages of the mating sequence.

Thus far, specific mental-gland pheromones have not been associated with specific VNO receptors, but it has been shown that mental-gland extracts and purified pheromones activate sensory neurons in the VNO and in the areas of the brain to which the VNO projects (reviewed in Woodley 2010). Beyond this, the mechanism of pheromone action in females is unknown, but exposure to mental-gland pheromones has been shown to have endocrine-priming effects in males. Males, but not females,

exposed to the mental-gland secretions of males showed increased levels of plasma corticosterone (Schubert et al. 2009). The hypothesized mechanism is that neurons projecting from the VNO stimulate the release of corticosterone. Corticosterone helps mobilize energy reserves in preparation for increased activity. During courtship, males are exposed to their own mental-gland secretions and thus release of corticosterone might serve a self-priming function (Schubert et al. 2009). Exposure to females' skin secretions also activates VNO receptors but does not cause increased release of corticosterone, however, which seems difficult to reconcile with the self-priming hypothesis (if increased corticosterone benefits males during courtship, why would they not respond in this way to secretions of females?). Another plausible function is that release of corticosterone might help males prepare for searching for intruders or for engaging in aggressive interactions when they encounter another male's scent.

Phylogenetic analysis of one mental-gland protein known as plethodontid receptivity factor (PRF) showed that it evolved 27 MYA in the Eastern *Plethodon* clade. The multiple genes coding for PRF exhibit extremely high levels of sequence divergence and high rates of evolutionary change at the amino-acid level. Up to 58% of the amino-acid sites in PRF are variable across species and some substitutions occur within, or near, sites known to be involved in receptor binding in similar molecules. Evidence for directional selection has been found at about 1 in 6 of PRF amino-acid positions (Palmer et al. 2005). The rapid evolution of PRF and other mental-gland proteins contrasts sharply with the highly conserved morphology and courtship behavior of this group (Watts et al. 2004; Palmer et al. 2005) and is hypothesized to be caused by coevolution of males' pheromones and females' receptors driven by sexual selection within species (Watts et al. 2004; but see Woodley 2010).

Given the high rate of divergence in the sequence of amino acids, it seems highly probable that mental-gland pheromones could be used by the salamanders for species recognition. They probably do not serve this role in male–female interactions, however, because they are applied to the female relatively late in the courtship sequence, after the stage at which species recognition is thought to occur (Houck 2009).

Birds

Competitor recognition in birds typically involves both visual and auditory cues. Which type of cue is dominant at close range depends on the species

(Lanyon 1963; Ratcliffe and Grant 1985; Tobias and Seddon 2009). Development of auditory cues (e.g., the song advertising the territory) and auditory recognition templates often involves learning (imprinting) during an early critical period (Marler 1991; Whaling et al. 1997). Constraints on learning and/or vocal performance may limit the potential targets for imprinting to closely related species. Birds that have imprinted on the song of a sympatric species may sing and respond to heterospecific song but still use visual cues at close range for recognizing conspecifics (Ratcliffe and Grant 1985). Imprinting can also result in a form of facultative character displacement, i.e., a cultural shift away from the song and from the song-recognition template of a sympatric species (Grant and Grant 2010).

Studying competitor recognition at the level of cues is relatively easy in birds because intrusion into a territory can be simulated in the field, using playbacks of territorial song. Many playback studies have employed experimentally manipulated song to isolate the components of the song that are required for species recognition. For example, Beletsky et al. (1980) found that the last syllable of red wing blackbirds' (*Agelaius phoeniceus*) song, a trill, is sufficient and necessary to elicit a territorial response. Experiments in which birds are presented with conflicting visual and auditory cues (e.g., conspecific song played back near a mounted specimen of a congener, or vice versa) have been used to determine which cues are used in species recognition. In a study of four tyrant flycatcher species (*Myiarchus* spp.), Lanyon (1963) found that each species responded aggressively only to conspecific song but would attack any mount presented simultaneously with conspecific song. While *Myiarchus* mounts were attacked more aggressively than non-*Myiarchus* mounts, no discrimination among *Myiarchus* mounts was detected. Lanyon (1963) inferred that competitor recognition within this morphologically homogenous genus is based only on song. In other cases, birds appear to use song at long range and visual cues at short range.

Matyjasiak (2005) studied a population of blackcap warblers (*Sylvia atricapilla*) that is interspecifically territorial against the closely related garden warbler (*Sylvia borin*). Dual-choice playback experiments, in which the territorial song of one of the two species was played from a speaker equidistant between mounted specimens of both species, were used to determine whether male blackcaps can distinguish between the territorial songs of the two species. Blackcaps usually directed aggression toward the mount matching the territorial song, which

confirmed that they can distinguish between the two types of territorial songs. This experiment also showed that the birds can associate species-specific visual and auditory cues. Matyjasiak (2005) suggested that this is a learned association, although the possibility that the birds make this association innately was not ruled out.

Several inferences about competitor recognition in birds have emerged from intensive long-term research on Darwin's finches (*Geospiza* spp.) in the Galapagos. Darwin's finches are territorial but only intraspecifically (the territories of sympatric species overlap). Although the territorial songs of some sympatric species are very similar, playback experiments revealed that males are able to distinguish among them. Males usually responded more aggressively to local conspecific song than to either heterospecific song or conspecific song from populations from other islands. An exception in which males responded strongly to heterospecific song involves two species that are known to compete for patches of *Opuntia* cactus (Ratcliffe and Grant 1985).

Male Darwin's finches normally learn to sing their father's song, but in rare cases of natural interspecific cross-fostering, males learn their foster father's song. Misimprinted males were more often seen in territorial chases with conspecifics than with the foster species, however, which suggests that visual cues override song at close range (Ratcliffe and Grant 1985). The results of dual-choice playback experiments also suggest that visual cues influence territorial responses at close range (Ratcliffe and Grant 1985).

In 1983, the large ground finch *Geospiza magnirostris* colonized the island of Daphne Major where two smaller ground finch species (*Geospiza scandens* and *Geospiza fortis*) were already established. *Geospiza magnirostris* is aggressive and socially dominant to the other species, and its territorial song falls within the same frequency band (2–4 kHz). As the population density of *G. magnirostris* increased, the territorial songs of the other two species diverged from *G. magnirostris* song in trill rate and in duration (Grant and Grant 2010). These shifts in song appear to be the result of an imprinting bias. Sons generally sang faster songs, and thereby differed more from *G. magnirostris*, than did their fathers (Fig. 2). The imprinting bias might be an example of the learning phenomenon known as "peak shift," which can arise when animals are trained to discriminate between two similar stimuli, only one of which is positively reinforced (ten Cate et al. 2006). Exactly how this would work in the case of the Darwin's finches is not clear. For example, do young male

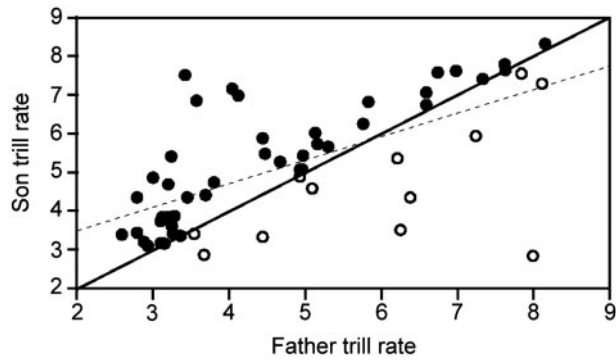


Fig. 2 Evidence for an imprinting bias in Darwin's finches (*Geospiza fortis*). The trill rate of sons is plotted against the trill rate of their fathers. The solid line has a slope of 1 and the dashed line is from regression analysis. Solid circles identify cases in which sons sang faster trills than did their fathers. The predominance of values above the solid line provides evidence for a "peak shift" away from a species that produces a lower trill rate (*G. magnirostris*). Reproduced from Grant and Grant (2010) with permission from Rosemary Grant.

G. scandens and *G. fortis* just need to hear *G. magnirostris* song or do they need to have aversive experiences (i.e., aggressive interactions) with *G. magnirostris*? It would also be pertinent to determine whether the shift in song reduces aggression from *G. magnirostris*. Answering such questions would require manipulative experiments of a sort that are not currently employed on Daphne Major, but perhaps they can be answered in other systems if the phenomenon proves to be general.

Experimental studies of cross-fostering have shown that imprinting plays a major role in the development of territorial song and in competitor recognition in tits (Paridae). Free-living territorial great tits (*Parus major*) and blue tits (*Cyanistes caeruleus*) that were raised by foster parents of the other species responded more aggressively to presentations of same-sex heterospecifics, and less aggressively to same-sex conspecifics, compared with noncross-fostered controls (Hansen and Slagsvold 2003). A follow-up study showed that the effects of cross-fostering on competitor recognition were permanent (Hansen et al. 2008). Cross-fostered great tits tend to be mixed singers who sing the song of both species. Playbacks of their songs elicited more aggressive responses from blue tit males, and less aggressive responses from great tit males, than did normal great tit songs (Hansen et al. 2010). Some cross-fostered tits paired up with conspecific mates and bred successfully. The offspring of such pairs have two conspecific parents, but at least one parent treats same-sex individuals of their foster species as

though they were competitors. This provided an opportunity to test for cultural transmission of competitor recognition from parent to offspring. No evidence for cultural transmission was found – the mature offspring of such pairs were no more aggressive to heterospecific intruders than were control birds that had been raised by two normal, conspecific parents (Hansen et al. 2007).

Reef fish

Territorial reef fishes have been reported to selectively attack other species with similar diets, whether or not they are closely related or similar morphologically (Ebersole 1977; Losey 1981, 1982). How do fish "know" which other species are competitors for food? Losey (1981, 1982) proposed that territory holders learn to recognize competitor species based on their feeding habits. To test this hypothesis, he carried out an elaborate aquarium experiment in which herbivorous territorial damselfish (*Stegastes fasciolatus*) were exposed to a tilapia species that they would never encounter in the wild (*Oreochromis mossambicus*). Some individual damselfish were repeatedly exposed to tilapia that had been trained to feed like herbivores while others were exposed to tilapia that had been trained to forage as zooplanktivores. Damselfish initially showed low levels of aggression toward tilapia, but over the course of the experiment, individuals that were exposed to herbivorous tilapia became more aggressive toward this species. Losey's (1982) experiment needs to be replicated on other species to determine the generality of the findings. To my knowledge, this remains the only experimental evidence that animals learn who their competitors are by observing their feeding habits.

Conclusions and promising directions for future research

- (1) Intraspecific competitor-recognition systems often involve multiple cues in the same, or different, sensory modalities. This means that there are multiple ways that competitor-recognition systems might evolve in response to selection for interspecific recognition. It also means that there may be some redundancy in competitor-recognition systems (e.g., intruders that are not identified visually might be identified by olfaction). Thus, errors made at one stage of an interspecific interaction might be corrected at a later stage.

- (2) While it seems likely that most interspecific recognition systems have evolved from intraspecific recognition systems, the same cues and templates are not necessarily used for intraspecific and interspecific recognition. For example, parabiotic ants appear to use different neural templates for recognizing their conspecific and heterospecific nestmates (Errard et al. 2008).
- (3) No predictable hierarchy of cues has emerged. One might expect long-range cues to be used for interspecific recognition and short-range cues to be used for intraspecific recognition, but the available examples do not always support this intuition. For example, *Eumeces* skinks use visual cues for sexual recognition and chemical cues for species recognition (Cooper and Vitt 1987, 1988). Which cues diverge in response to selection for interspecific recognition may depend on standing levels of variation in cues and templates prior to secondary contact and also on the level of divergence before contact. In the case of the skinks, prior to secondary contact the species might already have diverged in pheromones but not in coloration of the head.
- (4) Even in the simplest systems, there does not appear to be a direct stimulus–response relationship between the perceptual (template) and behavioral (action) components of competitor recognition. Context-dependent responses imply that there is an intervening motivational component. This complicates the interpretation of behavioral data and means that there are additional routes that evolution could take in response to selection for interspecific recognition besides shifts in cues and templates.
- (5) Competitor recognition appears to be at least partially learned, or otherwise acquired through experience, in the systems in which the development of competitor recognition has been studied. Imprinting during an early critical period has been shown to affect the development of competitor-recognition templates in ants and birds. Cues may also be modified by experience (e.g., CHC sharing in ants and song learning in birds). Some animals might learn who their competitors are through associative learning, but more research on this is needed. The ability to make such associations may be subject to selection.
- (6) Taxa in which the mechanisms of competitor recognition are best known offer opportunities to examine how competitor-recognition systems

evolve in response to selection for interspecific recognition (e.g., by comparing allopatric and sympatric populations). Cues that are products of genes (peptides, proteins) offer insights into rates of evolution. For example, do the pheromones that *Plethodon* salamanders use in territorial interactions evolve as rapidly as the pheromones that they use in courtship? Do such pheromones evolve more rapidly in sympatry than in allopatry? Across species, how well matched are templates and cues? Do animals always respond most aggressively to their own species-specific cues? To what extent is the current form of competitor-recognition templates a product of selection caused by interspecific aggression in the past?

- (7) From the standpoint of efforts to develop a predictive theoretical framework for studying evolutionary consequences of interspecific aggression (see Grether et al. 2009; Peiman and Robinson 2010), the complexity and diversity of competitor-recognition mechanisms is daunting. For models of agonistic character displacement to have much predictive value, they will need to incorporate taxon-specific details about perception, development, and motivation. Highly integrative, collaborative research efforts will be required to meet this challenge.

Acknowledgments

I thank Charles Derby and Richard Zimmer for organizing the Neuroecology symposium and Harold Heatwole and two anonymous reviewers for comments that greatly improved the manuscript.

Funding

Funding for the symposium was provided by the National Science Foundation (NSF), Biological Bulletin, the Society for Integrative and Comparative Biology, and the American Microscopical Society. My research on *Hetaerina* damselflies has been supported by grants from NSF (DEB-1020586) and the University of California Institute for Mexico and the United States (UC MEXUS).

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