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The role of interspecific interference competition in character displacement and the evolution of competitor recognition

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ABSTRACT

The extent to which interspecific interference competition has contributed to character evolution is one of the most neglected problems in evolutionary biology. When formerly allopatric species come into secondary contact, aggressive interactions between the species can cause selection on traits that affect interspecific encounter rates (e.g. habitat preferences, activity schedules), competitor recognition (e.g. colouration, song), and fighting ability (e.g. weaponry, body size). We define agonistic character displacement (ACD) as the process of phenotypic evolution in a population caused by interference competition with one or more sympatric species and which results in shifts in traits that affect the rate, intensity or outcome of interspecific aggression. After clarifying the relationships between ACD and other evolutionary processes that may occur when species come into secondary contact, we develop an individual-based, quantitative genetic model to examine how traits involved in competitor recognition would be expected to evolve under different secondary contact scenarios. Our simulation results show that both divergence and convergence are possible outcomes, depending on the intensity of interspecific exploitative competition, the costs associated with mutual *versus* unilateral recognition, and the extent of phenotypic differences prior to secondary contact. We then devise a set of eight criteria for evaluating putative examples of ACD and review the empirical literature to assess the strength of existing evidence and to identify promising avenues for future research. Our literature search revealed 33 putative examples of ACD across insects, fishes, bats, birds, lizards, and amphibians (15 divergence examples; 18 convergence examples). Only one example satisfies all eight criteria for demonstrating ACD, but most case studies satisfy four or more criteria. The current state of the evidence for ACD is similar to the state of the evidence for ecological character displacement just 10 years ago. We conclude by offering suggestions for further theoretical and empirical research on ACD.

Key words: character displacement, interference competition, interspecific territoriality, mistaken identity, misidentification theory, alpha selection, competitor recognition, species recognition, competitive mimicry, competitive interference.

CONTENTS

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I. INTRODUCTION

Interspecific exploitative competition is recognized as a potent mechanism of selection on traits that influence a species' ecological niche (see Section VIII: Glossary; Adams & Rohlf, 2000; Schluter, 2000*a*; Dayan & Simberloff, 2005). Much less attention has been paid to the evolutionary consequences of interspecific interference competition (see Section VIII; Peiman & Robinson, 2007). When formerly allopatric species come into secondary contact, the initial response of one species to the other is not likely to be adaptive, simply because the species have previously evolved in isolation from each other. Competitive interference between the species in the zone of sympatry may cause selection on traits that affect interspecific (1) encounter rates (e.g. habitat preferences, activity schedules), (2) competitor recognition (see Section VIII; e.g. colouration, song, response thresholds), and (3) fighting ability (e.g. weaponry, body size). The evolutionary dynamics of traits in the second category are particularly interesting.

If two species are in competition for a limiting resource, selection in sympatry may cause convergence in traits involved in competitor recognition because of the benefits of mutual recognition between true competitors (Cody, 1969, 1973). Conversely, if the species are not in competition for a limiting resource, the costs of accidental interspecific aggression may select for divergence in such traits (Lorenz, 1962, 1966). Although these ideas date back to the 1960s, there have been very few attempts to model or test them rigorously. Ironically, the same kinds of traits that are most useful for recognizing conspecific competitors have received a tremendous amount of attention in the context of sexual selection (Andersson, 1994; Kokko, Jennions & Brooks, 2006; Clutton-Brock, 2007). Most sexual selection research has focused on mate choice, but many traits classified as "ornaments" or "sexual signals" are known to play a role in intrasexual competitive interactions (Savalli, 1994; Berglund, Bisazza & Pilastro, 1996; Grether, 1996; Pryke & Andersson, 2003; Heinsohn, Legge & Endler, 2005; Setchell & Jean Wickings, 2005; Meyers *et al.*, 2006; Kraaijeveld, Kraaijeveld-Smit & Komdeur, 2007). The extent to which interspecific interference competition has contributed to the evolution of such traits is one of the most neglected problems in evolutionary biology (Fig. 1).

Here, we begin by clarifying the relationships among different evolutionary processes that may occur when species (especially congeners) come into secondary contact (Section II). We then focus specifically on the effects of interspecific aggression on the evolution of agonistic signals (Section III) and develop a simple model to examine how such signals and competitor recognition functions would be expected to evolve under different secondary contact scenarios (Section IV). Our simulation results show that both divergence and convergence are possible outcomes, depending on the intensity of interspecific exploitative competition. Next we devise a set of criteria for evaluating putative examples of agonistic character displacement (Section V) and review the empirical literature with the goals of assessing the strength of existing evidence and identifying the most promising avenues for further research (Section VI).

II. AGONISTIC CHARACTER DISPLACEMENT AND RELATED PROCESSES

Character displacement (Brown & Wilson, 1956) can be defined as a geographic pattern or as an evolutionary process, but using both types of definitions simultaneously is problematic because multiple patterns can result from the same process and multiple processes can result in the same pattern (Taper & Case, 1992*a*; Schluter, 2000*a*; Goldberg & Lande, 2006; Konuma & Chiba, 2007). We think the best solution is to define each form of character displacement as a process and describe the possible geographic patterns using more specific terms.

Two forms of character displacement are widely recognized: ecological character displacement (ECD) and reproductive character displacement (RCD). RCD can be defined as the process of phenotypic evolution in a population caused by cross-species mating and which results in enhanced prezygotic reproductive isolation between sympatric species. This process is known as reinforcement if speciation is incomplete and hybrids have low (but non-zero) fitness. Some authors prefer to use the term RCD only when hybrids are not produced or hybrid fitness is zero (reviewed in Coyne & Orr, 2004). For our purposes, however, this distinction is not crucial. For brevity, we use the term "RCD" to encompass

	Intrasexual	Intersexual
Intraspecific	Competition for mates & other resources	Mate choice & sexual conflict
Interspecific	Agonistic character displacement	Reproductive character displacement

Fig. 1. Some processes that may cause secondary sexual characters to evolve. Far more research effort has been devoted to intraspecific and interspecific–intersexual processes than to interspecific–intrasexual processes. Agonistic character displacement and reproductive character displacement are defined in Section II. (A shortcoming of this diagram is that competition need not be strictly intrasexual).

both reinforcement and post-speciation RCD. RCD may involve temporal isolation, habitat isolation, enhanced mate recognition, mechanical barriers to gamete transfer, and post-mating fertilization barriers.

ECD can be defined as the process of phenotypic evolution in a population caused by exploitative competition with one or more sympatric species and which results in shifts in traits that affect resource use. This definition does not encompass all phenomena that have at one time or another been referred to as ECD, but it is true to the original use of the term (see Section XI) and consistent with all existing theoretical models of ECD. ECD has been modeled in many ways, but all formal ECD models are based on differential resource utilization (exploitation) (e.g. Abrams, 1987*a*, Taper & Case, 1992*b*, Goldberg & Lande, 2006). Interference competition and other processes, such as predation, may influence the evolutionary outcome (see Abrams, 1986, 1987*b*), but the evolvable traits in ECD models (if explicit) are those that affect resource use. ECD can involve evolutionary shifts in body size, trophic traits (e.g. feeding apparatus), habitat preferences, and seasonality. Evolutionary shifts in the same traits could arise through other mechanisms and yield the same effects on resource use, but this would not qualify as ECD. For example, if cross-species mating caused a shift in body size, we would refer to this as RCD, not ECD, even if the shift in body size had trophic effects that reduced resource competition (cf. Konuma & Chiba, 2007). Clearly, multiple processes could contribute to any given phenotypic shift and separating them empirically can be difficult; our point is simply that the processes are conceptually distinct.

Interspecific interference competition alone may also cause character displacement (Adams, 2004, Peiman & Robinson, 2007), but there is no established general term for this process. Some authors have advocated broadening the definition of ECD to include interference competition (e.g. Adams, 2004), but recent reviews of ECD have placed interference competition in a separate category along with other processes, such as intraguild predation, that could generate similar patterns and therefore might be confused with exploitative competition (e.g. Taper & Case, 1992*a*, Schluter, 2000*a*, Dayan & Simberloff, 2005). Although interference mechanisms may themselves have evolved in response to past exploitative competition (Case & Gilpin, 1974, Gill, 1974), once evolved they affect the fitness landscape in ways that are distinctly different from resource depletion. Interspecific interference can also arise as a pleiotropic effect of other processes, including intraspecific competition (Schluter, 2000*b*, Gröning & Hochkirch, 2008). Like cross-species mating, interference competition could result in evolutionary shifts in traits (e.g. body size) that inadvertently affect resource use, but this is not the same process as ECD (Peiman & Robinson, 2007).

We define agonistic character displacement (ACD) as the process of phenotypic evolution in a population caused by interference competition with one or more sympatric species and which results in shifts in traits that affect the rate, intensity or outcome of interspecific aggression. Like exploitative competition, interference competition can have diverse effects. For example, interspecific aggression involves multiple stages at which selection could operate (encounter, detection, identification, pursuit, attack, *etc.*; Peiman & Robinson, 2007). Specific evolutionary responses may include temporal or spatial shifts in activity, improvements in competitor recognition, shifts in agonistic signals, and improvements in interspecific fighting ability. Just as RCD includes selection on both mate recognition functions and the traits upon which mate recognition is based (Coyne & Orr, 2004, Lemmon, Smadja & Kirkpatrick, 2004), ACD includes selection on both competitor recognition functions and the traits upon which competitor recognition is based.

Below, we focus on the effects of secondary contact on the evolution of traits involved in competitor recognition. In the Conclusions, we offer general predictions about the effects of interference competition on the evolution of niche separation and reproductive isolation (i.e. the interplay between character displacement processes).

III. INTERSPECIFIC AGGRESSION AND THE EVOLUTION OF AGONISTIC SIGNALS

Lorenz (1962, 1966) proposed that species- and age-specific colouration evolved in coral reef fishes because it enables territorial aggression to be directed exclusively towards conspecific competitors. No territorial coral reef fish, he argued, could afford to repel all intruders, and because of the high degree of niche specialization on coral reefs, there would be no advantage in doing so (but see Low, 1971, Ebersole, 1977; Ehrlich *et al.*, 1977; Neudecker, 1989). Meanwhile, ornithologists were debating the adaptive significance of interspecific territoriality in birds (e.g. Lanyon, 1959; Johnson, 1963; Ashmole, 1968). Orians & Willson (1964) argued that interspecific territoriality would be too costly to persist in the absence of benefits and that it may be adaptive when species that still overlap broadly in resource use come into secondary contact. Cody (1969, 1973) extended this line of reasoning and proposed that resource competition can select for convergence between species in agonistic signals (also see Moynihan, 1968). Although Lorenz's and Cody's hypotheses predict opposite geographic patterns (i.e. divergence *versus* convergence in agonistic signals), they can be reconciled by considering that selection favours individuals that distinguish between true competitors and classes of individuals that are not in competition for the same limiting resource. This puts the emphasis on competitor recognition (see Section VIII), as opposed to species recognition.

Gill (1974) introduced the term α-selection to refer to selection for enhanced interspecific competitive ability through interference mechanisms. When this results in specialized adaptations (behavioural, morphological, or chemical) for fighting with another species, it is distinct from the processes described by Lorenz (1962, 1966) and Cody (1969, 1973). Most empirical studies of α-selection, however, have focused on interspecific aggression *per se*. In this context, α-selection has often been contrasted with the hypothesis that interspecific aggression is a non-adaptive byproduct of intraspecific aggression (misidentification theory; Murray, 1981; Nishikawa, 1987; Adams, 2004). This too is best viewed as a competitor recognition problem. It is not robust to assume that selection in sympatry always favours increases in interspecific aggression over the allopatric condition, although this has often been presented as the α-selection prediction.

In a critique of Cody's hypothesis, Murray (1976) pointed out that competing species might not have to converge phenotypically to recognize each other as competitors. An analogous objection applies to Lorenz's hypothesis: species might not have to diverge further than they already have to recognize each other as non-competitors. Nevertheless, a shift in competitor recognition alone could have important consequences if, for example, it enabled two species to coexist by lowering the intensity of interspecific competition relative to intraspecific competition.

Our definition of agonistic character displacement (Section II) links all of these hypotheses together, for the first time, into a coherent conceptual framework.

IV. A COMPETITOR RECOGNITION-BASED MODEL

Here we develop a model that is meant to capture the essential elements of the evolutionary processes described by Lorenz (1962) and Cody (1969). This model could also serve as a platform for developing a more general model of ACD or models customized for particular systems.

(1) Scope and limitations of the model

Our primary goal is to determine whether the evolutionary trajectory of agonistic signals switches from divergence to convergence between species as the degree of exploitative competition increases. To test Murray's (1976) idea that shifts in competitor recognition might preempt shifts in agonistic signals, we also model the evolution of the recognition function. The model could allow for other forms of ACD, such as shifts in activity patterns or improvements in interspecific fighting ability, but we do not explore such alternatives herein. The model is not specific about the nature of exploitative competition and does not allow resource utilization traits to evolve (i.e. ECD is precluded). Likewise, the model does not permit cross-species mating, which precludes RCD. With our modeling approach, these assumptions could easily be modified to examine interactions among different character displacement processes.

(2) Specific assumptions

In the model, every individual pursues the same hawk-like strategy (Maynard Smith, 1982) of competing for territories/space (i.e. no floaters or sneakers). At each time step, each individual tries to keep or acquire a territory and encounters one opponent with probability p, where p equals the overall encounter rate. We do not model territoriality explicitly (i.e. spatially) but simply assume that the number of territories is limited and individuals can be classified, at a given point in time, as either residents or intruders. Encounters are random, i.e. the expected rate of encounter with individuals of each species and phenotype depends only on the density of each species and the distribution of phenotypes. No encounter in a particular time step means that the focal individual intruded on a vacant territory or already held a territory and no intrusion occurred. Competitor recognition is based on a phenotypic trait z, and the recognition function itself is defined by central location μ and width σ (i.e. the function peaks at μ). The probability that an individual with trait value z_1 is recognized as a competitor by an individual with μ_2 and σ_2 is 1.0 when $z_1 = \mu_2$ and decreases as z_1 departs from μ_2 following a Gaussian curve defined by σ_2. Whether an encounter results in a short or protracted territorial fight depends on whether recognition is mutual and therefore on both individuals' values of z, μ and σ. The model assumes no variation in fighting ability within or between species, and thus the probability of an individual winning a territorial fight is 0.5. W_{max} is the maximum expected fitness accrued in a given time step if no encounter occurs. Based on these assumptions, the possible outcomes of encounters and their associated fitness calculations are:

(1) Neither individual recognizes the other as a competitor (share territory). Fitness is calculated as $W = W_{max}/(E+1)$ where E is the degree of exploitative competition (1.0 for conspecifics, 0 for species that do not compete for a limiting resource, and intermediate values for species that partially overlap in resource use).

(2) Both individuals recognize the other as a competitor (fight). Winner takes territory, loser leaves. Both pay costs of fighting C_f. Winner's payoff is $W_W = W_{max} - C_f$. Losers payoff is $W_L = g{*}W_{max} - C_f$, where g is a value from 0 to 1 representing the expected fitness of a non-territory holder relative to a territory holder.

(3) Only one individual recognizes the other as a competitor (protracted fight). Winner eventually takes territory and loser leaves. Both pay costs of a protracted fight C_p. Winner's payoff is $W_W = W_{max} - C_p$. Losers payoff is $W_L = g^*W_{max} - C_p$.

$W_{ij}(t)$ is the reproductive success of individual *i* of species *j* in time step *t*, after taking into account the effects of exploitative competition or territorial fights. Lifetime fitness, the sum of $W_{ij}(t)$ across all time steps until death, stochastically determines the population density (n_j) and distribution of z_j, μ_j and σ_j in the next generation for each species.

The algorithm described above was embedded in a robust individual-based model with the following simplifying assumptions. For each species, z, μ and σ are unlinked, continuous traits (normally distributed at the start) and genetic variation is introduced only by mutation (no recombination or gene flow). Mortality is random with respect to phenotype (no survival selection), individuals are born mature and reproduce clonally, and generations are discrete (non-overlapping). It is possible that altering these assumptions could affect the results. For example, under some circumstances, survival selection on the agonistic signal might prevent character displacement from occurring. A strength of this modeling approach is that one could easily explore the effects of varying these and other factors.

We implemented the model using a computer program and systematically varied the degree of exploitative competition (E) and the cost of fighting associated with mutual recognition (C_f). In most biologically plausible scenarios, the cost associated with unilateral recognition (C_p) would equal or exceed the cost associated with mutual recognition (C_f), simply because interactions in which recognition is one-sided are likely to take more time and energy to resolve than interactions in which both individuals recognize each other as competitors. In our simulations, we varied C_f between zero and 1 while holding C_p constant at 1. Each simulation was run for 2500 generations, with up to four encounters possible per individual. For these simulations, we set the per trait, per generation mutation rate at 0.01 to ensure that there was sufficient phenotypic variation for natural selection to act on during the simulations. Each simulation began with 75 individuals of each species. Each species had a carrying capacity of 2000 individuals, and in all simulations the populations reached their carrying capacity within a few generations.

(3) Simulation results

With moderate amounts of pre-secondary contact divergence between the species (e.g. 1-3 standard deviations), the effects of varying the intensity of exploitative competition (E) are in line with the basic predictions of our extension of the Lorenz-Cody hypothesis. When there is no cost associated with sharing a territory with heterospecifics ($E = 0$), the species diverge from each other in both the agonistic signal (trait z) and the mean of the recognition function (μ) (upper left panel of Fig. 2). By contrast, when there is complete competitive overlap ($E = 1$), so that sharing a territory with heterospecifics is just as detrimental as sharing a territory with conspecifics, the species converge in both μ and z (lower left panel of Fig. 2). Between these extreme values of E, an abrupt shift from divergence to convergence occurs (at about $E = 0.5$ in upper right panel of Fig. 2).

With large amounts of pre-secondary contact divergence between the species (e.g. 10 standard deviations), divergence rarely occurs, even when the species are not competing ecologically (i.e. low E; lower right panel of Fig. 2). This is because the species already treat each other as non-competitors at the start. Convergence is also prevented, even when the species are strong ecological competitors (i.e. high E), if the cost associated with mutual recognition (C_f) is low relative to the cost associated with unilateral recognition (C_p) (lower right panel of Fig. 2). The latter result seems paradoxical when viewed only from the standpoint of heterospecific encounters, but it makes sense when the effects of conspecific encounters are considered. Convergence is prevented when the cost of failing to achieve mutual recognition with conspecifics exceeds the benefit of achieving unilateral recognition with heterospecifics. This is because a "convergent" mutant who deviates from its own species mean μ or mean z enough to achieve unilateral recognition with heterospecifics will be penalized by getting into protracted fights (or worse, sharing the resource) with conspecifics. The average fitness consequences of intraspecific and interspecific recognition will depend on the encounter rates with competitors of both species (approximately equal in our simulations). Presumably the species are more likely to evolve in response to each other as the interspecific encounter rate increases relative to the intraspecific encounter rate (see also Singer, 1989).

While these simulations explore only a small subset of biologically relevant parameter space, they serve to confirm that both convergence and divergence in agonistic signals are possible outcomes and that the outcome depends at least partially on the intensity of interspecific exploitative competition.

V. CRITERIA FOR AGONISTIC CHARACTER DISPLACEMENT

Evidence for character displacement falls into three basic categories: geographic patterns, *in situ* measurements of selection or mechanisms of selection, and manipulative experiments. Experiments manipulating phenotype distributions or species composition, combined with measurements of selection or responses to selection, provide the strongest tests of character displacement hypotheses (Schluter, 2000*a*; Gray & Robinson, 2002). The most frequently reported geographic pattern is a phenotypic shift in sympatry in comparison to allopatric populations of the same species. Other patterns that may be products of ACD include: a phenotypic shift along a gradient in relative abundance of two or more sympatric species (e.g. Tynkkynen, Rantala & Suhonen, 2004); a phenotypic shift along a gradient in the intensity of competition between sympatric species (e.g. Reed, 1982); and

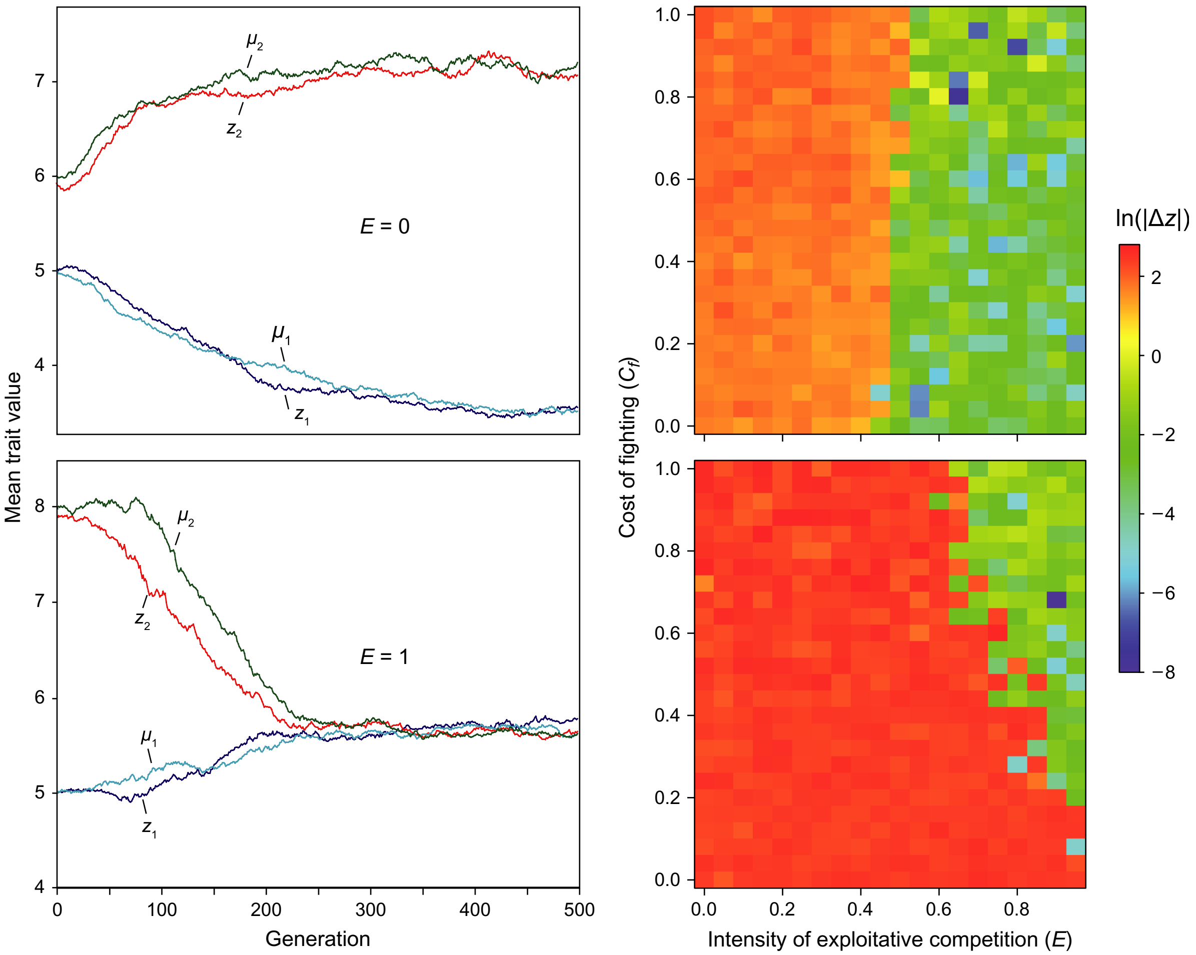

Fig. 2. Agonistic character displacement model simulation results. See Section IV for a description of the model and interpretation of these results. **Left:** Representative simulation runs showing divergence in the central location of a recognition function (μ) and the phenotypic trait on which recognition is based (z) between two species that do not compete exploitatively ($E = 0$; upper graph) and convergence in z and μ between two species that compete intensely for a limiting resource ($E = 1$; lower graph). **Right:** A graphical summary of two sets of simulations in which E and the cost of fights resulting from mutual recognition (C_f) were varied systematically from 0 to 1. The cost of fights resulting from unilateral recognition (C_p) was held at 1 in these simulations. Colours show the natural log of the mean difference between the species in trait z after 2500 generations. **Upper right:** here the starting mean values were $z = 5$ and $\mu = 5$ for species 1 and $z = 7.5$ and $\mu = 7.5$ for species 2 [initial mean $\ln(|\Delta z|) = 0.92$]. Red indicates divergence while the other colours represent different levels of convergence. An abrupt shift from divergence to convergence occurs near $E = 0.5$. **Lower right:** here the starting mean values were $z = 5$ and $\mu = 5$ for species 1 and $z = 15$ and $\mu = 15$ for species 2 [initial mean $\ln(|\Delta z|) = 2.3$]. In this case, red indicates stasis (because the species were already strongly divergent at the start of these simulations) and the other colours represent different levels of convergence. In all these simulations, the per-trait mutation rate was 0.01 and other parameter values were set as follows: maximum expected fitness in a time step if no encounter occurs $W_{max} = 5$; expected fitness of a non-territory holder relative to a territory holder $g = 0.7$. The mean values of the width of the recognition function σ_j were approximately 1.0 at the start and changed little throughout the simulations (not shown). In the simulations runs shown on the left, $C_f = 0.5$.

greater similarity (or dissimilarity) within sympatric species pairs compared with allopatric species pairs (e.g. Cody 1973; Diamond, 1982). For a more complete list of patterns that may be indicative of character displacement, see Goldberg & Lande (2006).

To build a convincing case that an observed geographic pattern was caused by a particular form of character displacement, it is important to show that the pattern (1) is at least partially genetic, (2) is unlikely to have arisen by chance, (3) represents evolutionary change, not differential extinction or merging, (4) persists after controlling for environmental variables other than the presence of the relevant species, (5) is not likely to be a pleiotropic effect of another evolutionary process, and (6) is not a product of hybridization. The first five criteria apply to most forms of character displacement (Schluter, 2000*a*), while the sixth criterion is relevant only for cases of possible convergence in sympatry. Two additional criteria apply specifically to

ACD: (7) evidence that the observed (or inferred) phenotypic shift affects the intensity of interspecific competitive interference in the predicted direction, and (8) independent evidence for interspecific interference competition. The first six criteria help evaluate whether an observed geographic pattern is likely to be a product of processes other than ACD and the last two criteria test for mechanisms specific to ACD. In our review of the literature, we evaluated the degree to which published studies fulfilled each criterion, with the following considerations.

(1) A common-garden experiment is usually the most direct way to determine whether a phenotypic difference between populations has a genetic basis. A complementary approach is to determine whether the same phenotypic shift can be induced by exposure to environmental factors that differ between sympatric and allopatric sites. Phenotypic plasticity itself may be a product of selection, however, and it is important to consider that norms of reaction may differ between sympatric and allopatric populations because of past interspecific competition (Rice & Pfennig, 2007). Thus, demonstrating that a phenotypic shift in competitor recognition or a territorial signal (e.g. bird song) involves learning does not automatically rule out genetic divergence. Such cases may require reciprocal translocation experiments, in which animals from allopatric sites are raised at sympatric sites and *vice versa*. Very few of the studies in our review were conclusive in this regard.

(2) At a minimum, addressing the second criterion requires replication of populations (or species) and a statistical test comparing the observed pattern to a random expectation (Adams & Collyer, 2007). Replicate populations may not be independent, however, because of gene flow or shared phylogenetic history. Showing that the same phenotypic shift has occurred in multiple secondary contact events is the most direct way to address this issue, but such opportunities are rare (Schluter & McPhail, 1993). When evaluating published studies, we simply asked whether any level of replication was achieved and, if so, whether the pattern was compared statistically to a random expectation.

(3) Differential extinction could lead to the same kinds of sympatry/allopatry patterns as ACD if phenotypic similarity affects coexistence. Likewise, differential merging (i.e. complete hybridization) could lead to the same kinds of sympatry/allopatry patterns as ACD if phenotypic similarity affects reproductive isolation. For population-level comparisons, we considered the third criterion to be met if the "displaced" trait means of populations in sympatry lie outside the range of trait means of the same species in allopatry. For species-level comparisons, we considered this criterion to be met if the displaced trait means lie outside the range of trait means of closely related allopatric species.

(4) Phenotypic shifts in sympatry can result from species evolving independently in response to the same (or different) environmental factors. We considered the fourth criterion to be tentatively met if the researchers attempted to control for the most obvious environmental factor(s). We considered shifts in competitor recognition alone (i.e. without a corresponding trait shift) to satisfy this criterion automatically.

(5) Convergent ACD is unlikely to be confused with other character displacement processes but it could be confused with protective or social mimicry (Moynihan, 1960, 1968). In protective mimicry, one or more species gains protection from predators by evolving to resemble an unpalatable or otherwise protected species (reviewed in Ruxton, Sherratt & Speed, 2004). Social mimicry refers to an evolved resemblance between species that facilitates the formation of mixed species groups (Moynihan, 1960). Whether these forms of mimicry offer a plausible alternative to convergent ACD depends on the study system. Divergent ACD can be confused with both ECD and RCD, and these processes are not mutually exclusive. For example, the colour shift of male pied flycatchers (*Ficedula hypoleuca*) in sympatry with collared flycatchers (*F. albicollis*) can be explained by both ACD (Alatalo, Gustafsson & Lundberg, 1994) and RCD (Saetre *et al.*, 1997, Saether *et al.*, 2007) (see below). In some cases, however, evolutionary processes other than ACD can be ruled out. We considered the fifth criterion to be met if competitor recognition is displaced in sympatry, because this strongly implicates interspecific aggression as the agent of selection.

(6) An additional challenge for convergent ACD is demonstrating that the pattern is not caused by introgression (i.e. increased similarity through post-secondary contact gene exchange). We considered this sixth criterion to be met if the species in question belong to different genera, but otherwise we checked for records of hybridization.

(7) Evidence that a phenotypic shift affects interspecific interactions in the predicted direction can be obtained in several ways. Phenotype manipulation experiments are probably the best way to determine whether shifts in territorial signals affect heterospecific responses. Observational data (i.e. correlations between trait values and responses) may be confounded by phenotypic condition or other factors. We rated published studies on whether they provided observational or experimental evidence that this criterion was met. We considered shifts in competitor recognition to meet this criterion automatically.

(8) Independent evidence for interspecific interference competition can take the form of natural history observations, measurements of interspecific aggression or territoriality in sympatry, or removal/addition experiments showing the impact of one species on the other.

VI. EMPIRICAL EVIDENCE FOR AGONISTIC CHARACTER DISPLACEMENT

We searched the literature for studies in which a role for interference competition in character displacement was suggested by the authors and evaluated the degree to which each study fulfilled the criteria above. Specifically, we searched online literature databases and obtained a list of papers citing Lorenz (1962, 1966), Cody (1969, 1973), or Gill (1974). The reference lists of these papers and key words were used to identify additional candidate studies. For inclusion in Table 1 and 2, criterion 7 or 8 had to be met, which excludes examples of patterns without evidence for interference competition. Examples of "convergence"

Table 1. Possible examples of divergence in competitor recognition or traits involved in competitor recognition. Below the table, we list the eight criteria required to demonstrate that a geographic pattern is a product of agonistic character displacement (ACD) and the codes used to denote particular kinds of evidence. Codes enclosed in parentheses identify contrary evidence. Species marked with an asterisks (*) are those showing a character displacement pattern. Geographic pattern codes: Intraspecific S/A = a within-species phenotypic shift between sympatric and allopatric populations; Intraspecific S/S = a within-species shift between different sympatric populations; Interspecific S/A = phenotypic displacement among sympatric species differs from that of allopatric species; Intraspecific RA = a within-species phenotypic shift between populations differing in the relative abundance of heterospecifics. n/a, not applicable; – indicates that the criterion has not yet been addressed.

			Alternatives examined						Evidence for ACD			
Species	Location	Trait	1	2	3	4	5	6	7	8	Geographic pattern	References
Calopteryx damselflies: *C. splendens** & *C. virgo*	Finland	Visual signals	CO	RS	–	–	–	n/a	SE	OB, AE	Intraspecific RA	Tynkkynen *et al.* (2004)
Benthic* & limnetic* Three-spined sticklebacks *Gasterosteus aculeatus*	Central N. America	Visual signals	CO	RS	EV	–	RX	n/a	–	OB	Intraspecific S/A	Albert *et al.*, (2007)
Lake Victoria haplochromine cichlids	East Africa	Visual signals	CO	RS	–	EA	EX	n/a	–	OB	Interspecific S/A	Seehausen & Schluter (2004)
Salamanders: *Plethodon metcalfi** & *P. teyahalee*	Appalachian Mountains, USA	Recognition (modality unknown)	–	–	–	–	–	(re)	–	AE, RM	Intraspecific S/S	Hairston (1983); Nishikawa (1987)
Dendrobatid frogs: *Allobates femoralis** & *Epipedobates trivittatus*	Amazon basin	Vocal recognition	–	RS	EV	CR	CR	n/a	CR	OB,AE	Intraspecific S/A	Amézquita *et al.* (2006)
Anolis lizards	American tropics	Visual signals	–	RS	–	–	—	n/a	–	OB	Interspecific S/A	Ord & Martins (2006)
Niveoscincus skinks: *N. microlepidotus** & *N. greeni*	Tasmania	Body size	–	RS	–	–	–	n/a	SE	OB,AE	Intraspecific S/A	Melville (2002)
Antbirds (family Thamnophilidae)	Neo-tropical lowlands	Vocal signals	–	RS	EV	EA	EX	n/a	–	OB	Interspecific S/A	Seddon (2005)
Ficedula flycatchers: *F. hypoleuca** & *F. albicollis*	Gotland	Visual signals	CO	RP	–	–	–	n/a	SE	OB	Intraspecific S/A	Alatalo *et al.* (1994)
Parus tits: *P. caeruleus** & *P. major*	Central Europe, N. Africa	Vocal signals	–	RS	EV	–	–	n/a	–	OB	Intraspecific S/A	Doutrelant & Lambrechts (2001)
Fringilla chaffinches: *F. coelebs** & *F. leydea**	Canary Islands	Vocal recognition	–	–	–	CR	CR	n/a	CR	OB	Intraspecific S/A	Lynch & Baker (1991)
Hetaerina damselflies: *H. americana**, *H. occisa**, *H. titia*	North America	Visual recognition	–	RS	–	CR	CR	n/a	CR	OB,AE	Intraspecific S/A	C.N. Anderson & G.F. Grether (unpubl. data)
Pogoniulus Tinkerbirds: *P. subsulphureus** & *P. bilineatus**	Central Africa	Vocal signals	–	RS	EV	EA	–	n/a	SE	OB, AE	Intraspecific S/A	Kirschel *et al.* (2009)
Rhinoceros beetles: *Chalcosoma caucasus** & *C. atlas**	Southeast Asia	Body size	–	RS	EV	EA	–	n/a	–	OB	Intraspecific S/A	Kawano (2002)

Rhinolophid bats; *Rhinolopus euryale** & *R. hipposideros**	Sardinia and southern Italy	Vocal signals	–	RP	EV	–	–	n/a	–	OB	Intraspecific S/A	Russo *et al.* (2007)

Codes used in Tables 1 & 2 for the eight ACD criteria: (1) The pattern is at least partially genetic: GE = trait displacement shown to have a simple (Mendelian) genetic basis; CG = genetic basis of displaced trait established through a common-garden experiment; CO = phenotypic shift involves coloration, which is unlikely to be plastic with respect to the presence or absence of a competitor; (gf) = high gene flow or short distance between sympatric and allopatric populations makes genetic divergence unlikely; (pl) = strong evidence for a role of plasticity (e.g. learning) but genetic divergence in reaction norm not ruled out. (2) The pattern is unlikely to have arisen by chance: RP = replicate sympatric and allopatric populations (or species) are considered without a formal statistical test to evaluate differences between sympatry and allopatry; RS = replicate sympatric and allopatric populations (or species) are considered, using a formal statistical test to evaluate differences between sympatry and allopatry. (3) The pattern represents evolutionary change, not differential extinction or population merging: EV = population means of the displaced trait in sympatry lie outside the range of variation present in allopatry. (4) The pattern persists after controlling for environmental variables other than the presence of the other species: CR = criterion satisfied by showing displacement of competitor recognition in sympatry; CS = opposite-sex control, i.e. one sex used as a control for environmental variation influencing variation in the other sex; EA = statistical effect of heterospecific presence/absence persists after controlling for environmental variation. (5) The pattern is unlikely to be a pleiotropic effect of another evolutionary process occurring in sympatry: CR = criterion satisfied by showing displacement of competitor recognition in sympatry; RX = reproductive character displacement is excluded as a potential explanation; EX = ecological character displacement is excluded as a potential explanation. (6) The pattern is unlikely to be a product of hybridization: NO = hybridization not reported and species are separated at the genus level or higher; NR = hybridization not reported in nature; (re) = Hybridization reported in nature; (on) = Hybridization ongoing in nature; (ex) = Hybridization extensive in nature. (7) Evidence that the observed (or inferred) phenotypic shift affects interspecific interactions in the predicted direction: CR = criterion satisfied by showing displacement of competitor recognition in sympatry; SE = staged encounters between species, without phenotypic manipulations, provide evidence that phenotypic shift affects interspecific aggression; PM = a phenotype manipulation experiment is used to show that the observed phenotypic shift affects interspecific aggression. (8) Independent evidence for interspecific interference competition: OB = observational evidence for interspecific aggression; ET = exclusive, non-overlapping interspecific territories observed; AE = experimental evidence for interspecific aggression (e.g. elicited by simulated intrusions); RM = strong evidence for interspecific interference competition through a removal experiment.

that are clearly attributable to shared ancestry or hybridization were not included.

(1) Divergent ACD

(*a*) *Summary*

Our review of the literature revealed several possible examples of divergence in competitor recognition or traits involved in competitor recognition (Table 1). No case study fulfills all of the criteria for divergent ACD, and only criteria 2 and 8 are satisfied in the majority of studies. A major impediment to demonstrating divergent ACD is that identical patterns are often predicted by RCD. Of the fifteen cases in Table 1, nine involve divergence in secondary sexual characters that are thought to play a role in mate choice as well as intrasexual competition. Nevertheless, it is clear that that interference competition has the potential to explain the divergence of agonistic signals and competitor recognition in a wide range of taxonomic systems and communication modalities.

(*b*) *Case studies*

The example that best illustrates the challenge in distinguishing between ACD and RCD is the geographic colour shift in pied flycatchers (*Ficedula hypoleuca*). At allopatric sites, male pied flycatchers are predominantly black and white, like the males of the competitively dominant collared flycatcher (*F. albicollis*), but where these species are sympatric, the dark patches on male pied flycatchers tend to be brown, like the females of both species. Compared to black males, brown males receive less aggression from collared flycatchers and are more successful in establishing breeding territories in preferred habitat; thus, the colour shift can be explained as a product of interspecific interference competition (Kral, Jarvi & Bicik, 1988; Saetre, Kral & Bicik, 1993; Alatalo *et al.*, 1994). The same colour shift has also been attributed to reinforcement. At allopatric sites, female pied flycatchers prefer black males, but in sympatry with collared flycatchers they prefer brown males, apparently because of selection against hybrid offspring (Saetre *et al.*, 1997; Saether *et al.*, 2007). It is not clear whether the colour shift of pied flycatchers was caused by ACD, RCD, or by both processes.

RCD can be rejected in one case of secondary sexual character divergence, although other explanations involving female choice and environmental gradients have not been ruled out. Albert, Millar & Schluter (2007) demonstrated a character displacement pattern in the nuptial colouration of threespine sticklebacks (*Gasterosteus aculeatus*) by showing that males in three allopatric (one-species) lakes are intermediate in red colour intensity between the "limnetic" and "benthic" species in sympatric (two-species) lakes. Reinforcement can be ruled out as an explanation for this pattern because both benthic and limnetic females show a directional preference for males with more intense red colouration (Boughman, 2001; Boughman, Rundle & Schluter, 2005). Sexual selection driven by habitat differences in water colour or light intensity offers a possible

Table 2. Possible examples of convergence in competitor recognition or traits involved in competitor recognition. For a list of the codes used to denote particular kinds of evidence, see Table 1. For criterion 6, hybridization status for birds was checked in McCarthy, 2006.

Species	Location	Trait	Alternatives examined						Evidence for ACD		Observed pattern	References
			1	2	3	4	5	6	7	8		
Sticklebacks: *Culaea inconstans** & *Pungitius pungitius*	Ontario, Canada	Recognition (modality unknown)	CG	RS	EV	CR	CR	NO	CR	AE	Intraspecific S/A	Gray & Robinson, (2002); Peiman & Robinson (2007)
Three-spined stickleback *Gasterosteus aculeatus** & Olympic uudminnow *Novumbra hubbsi*	Washington, USA	Visual signals	GE	–	EV	–	–	NO	SE	–	Intraspecific S/A	Hagen *et al.* (1980); Scott & Foster (2000)
Picoides woodpeckers: *P. pubescens* & *P. villosus*	N. America	Visual signals	CO	–	–	–	–	NR	–	OB	Intraspecific S/A	Jackson & Ouellet (2002); Weibel & Moore (2005)
Empidonax flycatchers: *E. alnorum** & *E. traillii**	Ontario, Canada	Vocal recognition	–	–	–	CR	CR	(re)	CR	OB, AE, ET	Intraspecific S/A	Prescott (1987)
Orioles (*Oriolus* spp.)* & friarbirds (*Philemon* spp.)	Wallacea, New Guinea	Visual signals	CO	RP	EV	–	–	NO	–	OB	Interspecific S/A	Diamond (1982)
Chaffinch *Fringilla coelebs** & great tit *Parus major**	Scotland	Vocal recognition	(gf)	–	–	CR	CR	NO	CR	OB, AE, ET, RM	Intraspecific S/S	Reed (1982)
Certhia treecreepers: *C. brachydactyla** and *C. familaris*	Spain	Vocal recognition	–	–	–	CR	CR	(on)	CR	OB,AE	Intraspecific S/A	Gil (1997)
Acrocephalus warblers: *A. scirpaceus** and *A. palustris*	Germany	Vocal recognition	–	–	–	CR	CR	(on)	CR	OB, AE	Intraspecific S/A	Catchpole (1978)
Acrocephalus warblers: *A. scirpaceus** and *A. arundinaceus*	Germany	Vocal recognition	(gf)	–	–	CR	CR	(re)	CR	OB, AE	Intraspecific S/A	Catchpole & Leisler (1986)
Passerina buntings: *P. cyanea** and *P. amoena**	Central N. America	Vocal signals	(pl)	RP	EV	–	–	(ex)	–	OB, AE, ET	Intraspecific S/A	Emlen *et al.* (1975)
Passerina buntings: *P. cyanea** and *P. amoena**	Central N. America	Vocal recognition	(pl)	RP	–	CR	CR	(ex)	CR	OB, AE, ET	Intraspecific S/A	Emlen *et al.* (1975); Baker, (1991)
Luscinia nightingales: *L. luscinia** and *L. megarhynchos*	Europe	Vocal signals	(pl)	RP	EV	–	EX	(ex)	SE	OB, ET, AE	Intraspecific S/A	Sorjonen (1986)
Emberizid finches: *Pipilo ocai* and *P. erythrophthalamus*	Mexico	Vocal signals	–	–	–	–	–	(ex)	–	OB, ET	Intraspecific S/A	Cody & Brown (1970)
Emberizid finches: *Pipilo ocai* and *Atlapetes brunneinucha*	Mexico	Visual signals	–	–	–	–	–	NO	–	OB, ET	Intraspecific S/A	Cody & Brown (1970)
Luscinia nightingales: *L. luscinia** and *L. megarhynchos*	Europe	Vocal recognition	–	RP	–	CR	CR	(ex)	CR	OB, ET, AE	Intraspecific S/A	Sorjonen (1986)
Phoenicurus redstarts: *P. ochuros** and *P. phoenicurus*	Czech Republic	Vocal recognition	(gf)	–	–	CR	CR	(ex)	CR	OB, ET, AE	Intraspecific S/A	Sedlacek *et al.* (2006)
Meadowlarks: *Sturnella magna** and *S. neglecta**	Central N. America	Visual signals	CO	RP	–	CS	–	(on)	–	OB, AE, ET	Intraspecific S/A	Lanyon (1957); Rohwer (1973)
Meadowlarks: *Sturnella magna** and *S. neglecta**	Central N. America	Vocal recognition	(pl)	–	–	CR	CR	(on)	CR	OB, AE, ET	Intraspecific S/A	Lanyon (1957); Falls & Szijj (1959); Rohwer, (1973); Ordal (1976)

explanation (Boughman, 2001; Boughman *et al.*, 2005; Albert *et al.*, 2007). Interspecific interference competition is a plausible alternative because interspecific aggression over nesting sites occurs, with limnetic males tending to get displaced by the larger benthic males (Rowland, 1989). Whether limnetics with more divergent colouration receive less aggression from benthics remains to be determined.

Geographic evidence for ACD can take the form of a phenotypic shift along a gradient in the relative abundance of sympatric species. *Calopteryx splendens* and *C. virgo* are sympatric damselflies in which the males display blue-black wing spots and compete for mating territories. The wing spots of *C. virgo* are uniformly large while those of *C. splendens* vary both within and among populations. Tynkkynen *et al.* (2004) found that the average wing spot size of *C. splendens* decreased with increasing relative abundance of *C. virgo*. Subsequent research showed that *C. virgo* males have greater territory-holding ability than *C. splendens* males, that *C. virgo* males are most aggressive towards *C. splendens* with relatively large wing spots, and that selection on the size of the wing spots of *C. splendens* is affected by *C. virgo* removal (Tynkkynen *et al.*, 2004, 2005, 2006). In combination, these results provide a strong case for divergent ACD. RCD is a plausible alternative explanation for the geographic pattern, however. Male *Calopteryx* damselflies perform courtship displays and there is evidence that females choose males on the basis of wing colouration (Siva-Jothy, 1999; Cordoba-Aguilar, 2002; Svensson *et al.*, 2007). Whether female choice in *C. splendens* shifts in response to the relative abundance of the two species should be examined. It also remains to be shown that variation in the relative abundance of these two species is stable enough to have evolutionary effects.

Four examples in Table 1 involve divergence in competitor recognition functions and thus escape the potentially confounding influence of RCD. For example, males of the poison dart frog *Allobates femoralis* have narrower frequency response curves (Fig. 3) at sites where this species co-occurs with *Epipedobates trivittatus,* which calls at a similar but lower frequency than *A. femoralis,* compared to sites where *E. trivittatus* is absent (Amézquita *et al.*, 2006). Amézquita *et al.* (2006) also tested for but did not detect a corresponding shift in the calls of *Allobates femoralis*. This is one of the few studies to investigate geographic variation in both agonistic signals and response functions. In another example of divergence in competitor recognition, territorial males in the damselfly genus *Hetaerina* use species differences in wing coloration to discriminate between conspecific and heterospecific intruders in sympatry but not in allopatry (C. N. Anderson & G. F. Grether, unpublished data). That is, competitor recognition functions are narrower in sympatry. Whether the underlying proximate mechanisms in these examples involve genetic divergence or adaptive phenotypic plasticity remains to be determined.

The most frequently cited example of α-selection may instead be an example of divergence in competitor recognition. Hairston (1983) used removal and translocation experiments to study interspecific competition between plethodontid salamanders in the Appalachian Mountains. He found that the *per capita* negative effect of one species on another (α) differs between mountain ranges and further deduced that a change in interspecific interference, not niche partitioning, was responsible for the shift in α (see also Hairston; Nishikawa & Stenhouse, 1987). Nishikawa (1987) brought salamanders from the same localities into the laboratory and measured levels of aggression in staged encounters between "residents" and "intruders". In the Great Smoky Mountains, where Hairston (1983) found strong interspecific competition, residents of both species were highly aggressive but did not discriminate between conspecific and heterospecific intruders. In the Balsam Mountains, where interspecific competition is weaker, one species (now called *P. metcalfi*) displayed less aggression to heterospecifics than to conspecifics while the other species

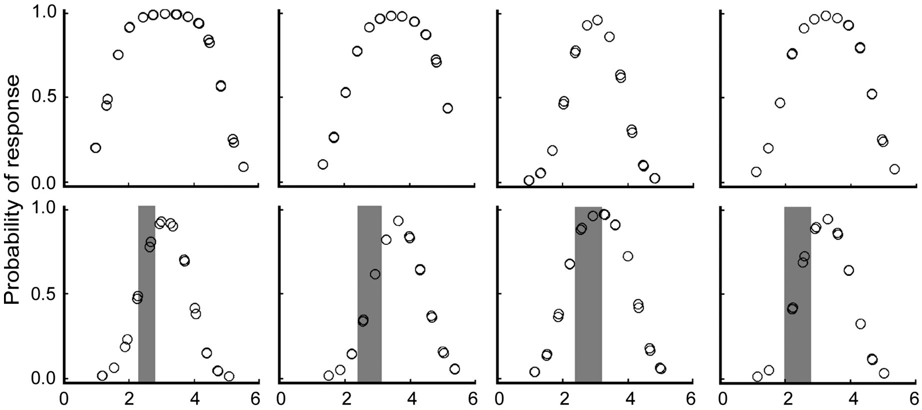

Fig. 3. Geographic variation in competitor recognition functions of the dendrobatid frog *Allobates femoralis*, as measured from territorial responses to playback of synthetic calls of varying frequency. The frequency-response curves of *A. femoralis* are significantly narrower at sites where another dendrobatid with an overlapping call frequency, *Epipedobates trivittatus,* is present (bottom row) than where it is absent (top row). Grey bands show the call frequency range of *E. trivittatus*. Modified from Amézquita *et al.* (2006) (reproduced by kind permission John Wiley & Sons). [Correction added on 12 October 2009 after first online publication: '(permission pending)' was replaced by '(reprinted with permission of John Wiley & Sons, Inc.)'].

(now called *P. teyahalee*) was less aggressive in general and did not discriminate between conspecifics and heterospecifics. Nishikawa (1987) interpreted these results as supporting Hairston's (1983) inference that interspecific interference had increased in the Great Smoky Mountains through α-selection. However, if one assumes that a lack of species discrimination represents the ancestral (secondary contact) condition, then the inferred shift in α could have been caused by *P. metcalfi* evolving the ability to distinguish between conspecifics and heterospecifics in the Balsams. These species do not seem to compete for a limiting resource (Hairston *et al.*, 1987), and thus it seems more likely that selection would favour a reduction in interspecific aggression than an escalation.

Table 1 only includes examples for which the researchers suspected a role for interference competition in driving divergence, but some putative cases of RCD may actually be cases of ACD. For example, character displacement patterns in chemical signals have often been interpreted as examples of RCD (Smadja & Ganem, 2005, 2008, Symonds & Elgar, 2008), but given that scent marks may be used to advertise territory ownership and competitive ability (Hurst & Beynon, 2004), ACD may provide a plausible alternative explanation for the patterns. We encourage researchers who have interpreted their results as evidence for RCD to consider whether ACD is a viable alternative.

(2) **Convergent ACD**

(*a*) *Summary*

Our review of the literature revealed several compelling examples of convergence in competitor recognition or traits involved in competitor recognition (Table 2). Taken together, they provide a strong case for further research on this phenomenon. Most examples involve passerine birds, but this might be an artifact of research effort rather than an indication of the true taxonomic distribution of convergent ACD. Recognition functions have more often been the subject of investigation than have agonistic signals. This imbalance likely reflects the relative ease of simulating territory intrusion with vocal playback in birds. Few examples satisfy criterion 1 (genetic basis). Oscine passerines learn their songs, and song recognition also shows substantial plasticity (e.g. Richards, 1979; Whaling *et al.*, 1997; Hansen & Slagsvold, 2003). Song convergence in sympatric buntings (*Passerina* spp.), for example, seems to result at least partially from the incorporation of heterospecific song phrases (Emlen, Rising & Thompson, 1975). As noted above, however, showing that a phenotypic shift involves learning does not rule out a genetic component to the shift because learning capabilities themselves can evolve. Common-garden or translocation experiments could help resolve this issue.

A general problem with demonstrating convergent ACD is that hybridization can yield a very similar pattern. The two processes may be indistinguishable without substantial behavioural or genetic evidence showing that hybridization does not occur. Putative examples of ACD for which hybridization appears to be the most plausible explanation are not considered further in this review (e.g. *Streptopelia* doves: de Kort & ten Cate, 2001; de Kort, den Hartog & ten Cate, 2002; den Hartog, de Kort & ten Cate, 2007; *Hippolais* warblers: Secondi, Faivre & Kreutzer, 1999; Secondi *et al.* 2003).

(*b*) *Case studies*

The contact zone between eastern and western meadowlarks (*Sturnella magna* and *S. neglecta*) in central North America is a classic example of character convergence. These species hybridize infrequently and have highly divergent territorial songs, yet they appear to occupy exclusive interspecific territories in sympatry (Lanyon, 1957, 1979; Rohwer, 1972, 1973). Rohwer (1973) showed that two male plumage characters appear to converge in the sympatric zone: the size of the black "V" marking on the breast and the yellow colour of the breast plumage (Fig. 4). Songs do not appear to have converged in sympatry (Ordal, 1976), but male meadowlarks respond to playbacks of heterospecific song more strongly in sympatry than in allopatry (Rohwer, 1973). This classic example has shortcomings, however. While population differences in plumage are likely to be genetically based, the same cannot be said for population differences in responses to song. Rohwer (1973) did not control for environmental gradients in his analysis of plumage differences between sympatric and allopatric meadowlarks (save using female plumage as a quasi control). Further behavioural research is also needed to establish whether plumage convergence results in improved heterospecific competitor recognition in sympatry.

Diamond (1982) presented compelling evidence that several species of oriole (*Oriolus* spp.) in the Indonesian archipelago are visual mimics of sympatric friarbirds (*Philemon* spp.). He proposed that orioles may gain two distinct, non-mutually-exclusive benefits from mimicking the friarbirds. First, they may escape aggression from the friarbirds, which drive smaller birds from shared feeding trees but seldom attack conspecifics or mimetic orioles. Second, by mimicking the larger, more aggressive friarbirds, orioles may be more effective at excluding other competing species. Either way, this system may be considered a putative case of convergent ACD as well as competitive mimicry (*sensu* Rainey & Grether, 2007). The proposed benefits of mimicry in this system are quite different from those of Cody's (1969) hypothesis: rather than honestly advertising their identity to facilitate interspecific spacing, orioles may deceive their competitors with mimetic colors. Additional research on this system is needed to rule out other possible explanations for the pattern and to determine whether orioles benefit from resembling friarbirds in the ways that Diamond (1982) suggested.

Chaffinches (*Fringilla coelebs*) and great tits (*Parus major*) co-occur across much of Europe, where they typically coexist without aggression in highly overlapping territories. On some islands, however, these species are interspecifically territorial, and their territories do not overlap (Reed, 1982). The islands have simpler vegetation structure than the mainland, which may force the two species to compete

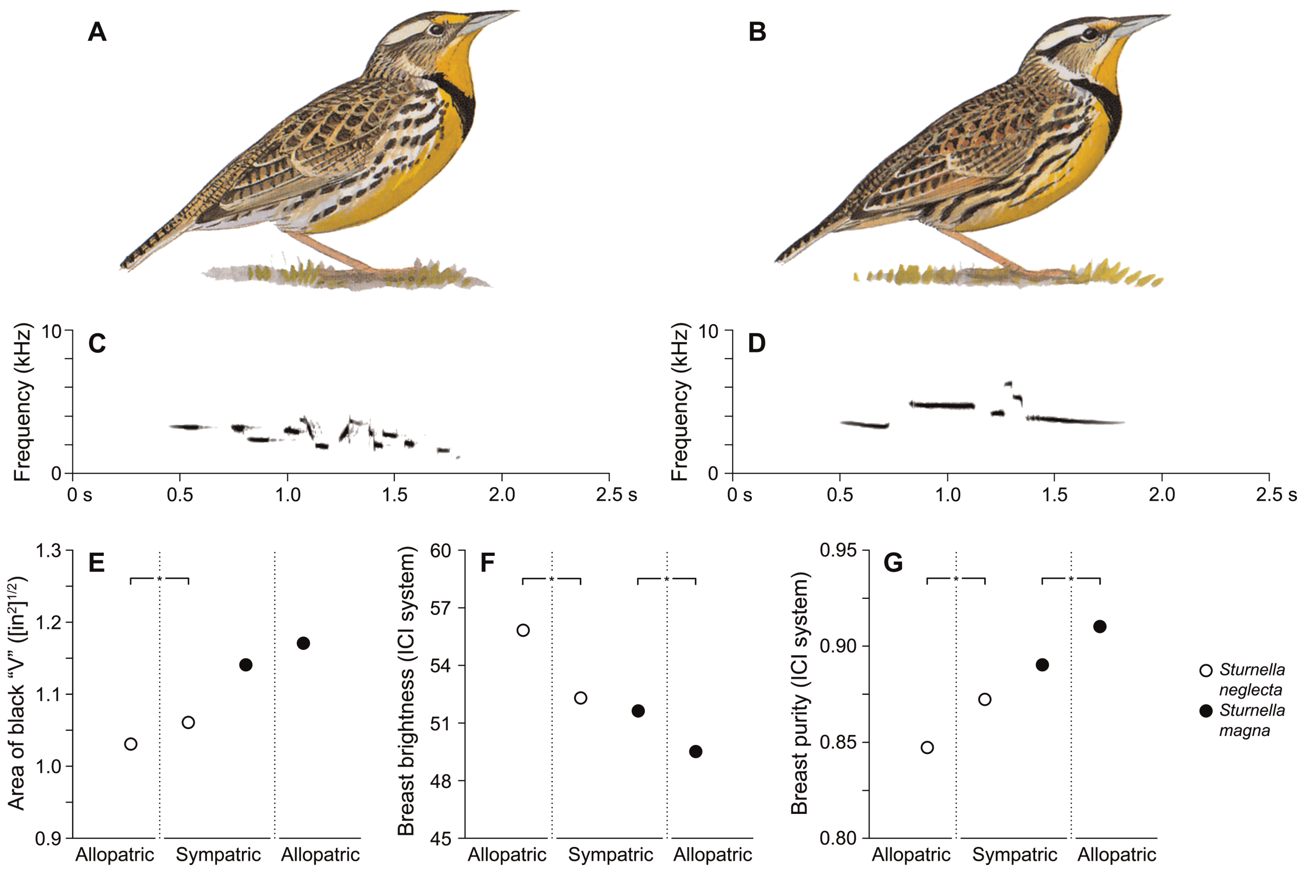

Fig. 4. North American meadowlarks show convergence in breast colour in sympatry. Western *Sturnella neglecta* (A, C) and Eastern *S. magna* (B, D) meadowlarks are remarkably alike in plumage but different in song. Rohwer (1973) showed that sympatric meadowlarks have converged in the size of the black "V" marking on their breast (E), as well as two measures of the yellow colour on their breasts (F, G). In E-G, * = significant contrast at $P = 0.05$. Data for E-G from Rohwer (1973) with permission from the author; spectrograms made from field recordings by N.L., and illustrations by permission of Alfred A. Knopf, a division of Random House. [Correction added on 12 October 2009 after first online publication: 'by D. A. Sibley (permission pending)' was replaced by 'by permission of Alfred A. Knopf, a division of Random House'].

more intensely for food or nest sites on the islands. Reed (1982) conducted song playback experiments at mainland and island sites in Scotland. Territory holders of both species responded to playbacks of the other species' song on the island but not on the mainland. When chaffinches were removed from part of the island, great tits significantly increased the size of their territories, expanding into areas formerly occupied by chaffinches (Reed, 1982). Because of the close proximity of mainland and island sites in this study (8 km), it seems unlikely that the site differences in competitor recognition are genetic, but this remains to be determined.

One case study meets all of our criteria for convergence in competitor recognition. In Ontario, brook sticklebacks (*Culaea inconstans*) occur both in sympatry and allopatry with the ninespine stickleback (*Pungitius pungitius*). In sympatry, the species have diverged somewhat in feeding niche but still appear to compete for resources (Gray & Robinson, 2002; Gray, Robinson & Parsons, 2005). In laboratory experiments on wild-caught adult fish, sympatric brooks show greater aggression toward ninespines than do allopatric brooks (Peiman & Robinson, 2007). Peiman & Robinson (2007) raised brooks from eggs in a common environment and found genetic differences in aggression between allopatric and sympatric populations but not between replicate populations within these categories. The researchers inferred that heterospecific aggression of brooks toward ninespines predates secondary contact (because even allopatric brooks are aggressive toward ninespines) and that α-selection led to the evolution of heightened heterospecific aggression in sympatry (Peiman & Robinson, 2007). We see this as equivalent to hypothesizing that competitor recognition was enhanced in sympatry. While it has not been demonstrated that heightened heterospecific aggression, *per se*, has increased the ability of sympatric brooks to compete for resources with ninespines, a field enclosure experiment showed that sympatric brooks grow more rapidly in the presence of ninespines than do allopatric brooks (Gray & Robinson, 2002).

Taken together, the cases described above and other examples in Table 2 provide strong empirical evidence for convergent ACD. The systems presented in Table 2 are the best-studied cases, but they are not the only ones. Cody (1969, 1973) presented several other candidate cases of character convergence, and Diamond (1982) pointed to other systems that may be similar to the oriole/friarbird system discussed above. None of these examples yet satisfy criterion 7 or 8, however. More work needs to be done to explore putative cases of convergent ACD, especially in non-avian systems.

VII. CONCLUSIONS

(1) Together, Lorenz's (1962) and Cody's (1969) hypotheses held the potential to explain a considerable amount of variation among species in agonistic signals. What became of these ideas? Some early papers reported that Lorenz's (1962) hypothesis does not apply to particular species of coral reef fish (e.g. Low, 1971; Ebersole, 1977, Ehrlich *et al.*, 1977; Neudecker, 1989), but more recent studies provide support for the hypothesis in other taxa (Table 1). Similarly, several of Cody's (1969, 1973) original avian examples were shown not to be valid cases of convergence in sympatry (Murray, 1976), but other examples remain plausible and several new examples have appeared (Table 2). Thus far, only one study, on brook sticklebacks, satisfies all eight criteria for ACD, but several studies satisfy four or more criteria (Tables 1 & 2). This situation is not drastically different from the state of the evidence for ECD at the time of Schluter's (2000*a*) review, which seemed to reinvigorate and also increase the rigor of research on ECD. We hope that the present review has the same effects on the study of ACD.

(2) Perhaps the most serious shortcoming of the current evidence for ACD is that, in the vast majority of cases, it is unclear whether the shift in agonistic signals or competitor recognition has a genetic basis (Table 1). Laboratory common-garden experiments and field translocation experiments are needed to address this issue. Environmental manipulations can also be informative, but it is critical to take into account that norms of reaction can diverge genetically among populations. Demonstrating that a particular phenotypic shift involves plasticity (e.g. learning) does not rule out a genetic component to the shift.

(3) The modeling approach that we have previewed here goes beyond optimality models of interspecific territoriality (e.g. Cody, 1973; Mikami & Kawata, 2004) by considering the coevolution of agonistic signals and competitor recognition functions across two species. We found that high exploitative competition between species readily facilitates convergence in both the agonistic signal and the competitor recognition function, as originally hypothesized by Cody (1969, 1973), while low exploitative competition favours divergence in both the agonistic signal and the competitor recognition function, as hypothesized by Lorenz (1962, 1966). This was true except when the species were already strongly divergent (and largely outside each other's recognition range) at the start of the simulation. In this scenario, convergence was inhibited when the cost associated with mutual recognition was low relative to the cost associated with unilateral recognition. This result can be understood by considering the fate of a mutant with a convergent agonistic signal (or recognition function) that is recognized by (or recognizes) heterospecifics but is not recognized by (or does not recognize) conspecifics. For such a mutant to be successful, the average benefit of achieving unilateral recognition with heterospecifics must exceed the average cost of failing to achieve mutual recognition with conspecifics (weighted by the relative encounter rates).

(4) Is displacement of competitor recognition more common than displacement of agonistic signals, or *vice versa*? Are these are usually alternative or co-occurring outcomes? The analogous question has occasionally been raised in the RCD literature (e.g. Hobel & Gerhardt, 2003; Lemmon *et al.*, 2004). Unfortunately our literature review was not very informative in this regard because most ACD studies did not test for shifts in both competitor recognition functions and agonistic signals. In our model simulations, the agonistic trait and recognition function usually tracked each other closely. More complex models (e.g. allowing for multiple "peaks" of recognition) should be explored to determine the generality of this finding.

(5) Shifts in competitor recognition are reported as frequently as shifts in agonistic signals, but the former usually involves convergence in sympatry while the latter usually involves divergence in sympatry (Tables 1 & 2). We suspect that this pattern merely reflects a bias in research effort. Most divergence studies involve testing for geographic shifts in visual signals, while most convergence studies involve testing for shifts in song recognition. Future studies should attempt to test for both kinds of shifts. While it is particularly easy to test for vocal recognition (using vocal playbacks to simulate territory intrusion), there are several ways to test experimentally for recognition of visual signals as well (e.g. video playback, model presentation, live animal presentation). We are not aware of any examples of ACD involving chemical signals, but the relative ease of using scent to simulate territory intrusion suggests that this would be a promising avenue for future research.

(6) Another important direction for future theoretical and empirical work is to study interactions between ACD and other evolutionary processes. When the same traits are used for both mate recognition and competitor recognition (e.g. Hawaiian cricket song; Mendelson & Shaw, 2006), how does interspecific interference competition affect the evolution of prezygotic isolation and thus speciation? We predict that ACD and RCD are mutually reinforcing processes if the species are not in competition for a limiting resource but antagonistic processes if the species are in competition for a limiting resource. Thus, for example, sympatric species in which males only defend mating territories might diverge more rapidly in secondary sexual traits than sympatric species in which males defend all-purpose territories.

The relationship between ACD and ECD probably depends on how interference competition affects resource use. To the extent that interspecific territoriality reduces exploitative competition, it weakens divergent selection on resource exploitation traits (Ashmole, 1968) and thus convergent ACD may prevent ECD from occurring.

The interaction between ACD and within-species sexual selection also warrants study. On the one hand, strong sexual selection on secondary sexual characters might prevent ACD from occurring in the same traits. On the other hand, ACD might perturb secondary sexual traits away from their sexually selected optima at sympatric sites. Evidence that RCD can have this effect on secondary sexual characters was provided by an elegant experimental evolution study on *Drosophila serrata* (Higgie & Blows, 2008).

(7) Most putative examples of divergent ACD are complicated by female choice and might, upon further study, prove to be cases of RCD, but the reverse also seems likely. This is primarily a concern for shifts in secondary sexual characters and temporal or spatial shifts in activity. It is conceivable, however, that mate recognition and competitor recognition functions are linked through pleiotropy, such that selection on one could result in evolutionary changes in the other as a correlated response. If so, this would make distinguishing between these processes quite challenging.

VIII. GLOSSARY

Agonistic signal: any phenotypic trait that conveys information about an individual's status as a potential competitor and influences the behaviour of some class of receivers in an interference competition context (examples include territorial song and conspicuous age-, sex- or species-specific colouration). This definition does not require the informative aspect of the trait (e.g. species-specificity) to have evolved because of the effect it has on the behaviour of receivers and thus includes "cues" as well as true signals (Hasson, 1994, Maynard Smith & Harper, 1995).

Competitor recognition: the identification of and discrimination among different classes of individuals in relation to the level of exploitative competition (inferred operationally from behavioural responses to intruders of different classes).

Exploitative competition: indirect, mutually negative interactions among individuals through depletion of a common, limiting resource.

Interference competition: any harmful interaction among individuals over access to a resource, whether or not the resource is limiting (Park, 1962, Krebs, 2001). Interspecific territoriality, for example, qualifies as interference competition whether it affects access to a resource used by both species (e.g. food) or a species-specific resource (e.g. mates).

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XI. APPENDIX

Here we explain our decision to introduce the term agonistic character displacement (ACD) instead of expanding the definition of ecological character displacement (ECD) to include trait shifts caused by interspecific interference competition. Some authors have suggested that ECD was not originally defined as being caused by exploitation alone, and so we first address this misconception.

Brown & Wilson (1956) coined the term "character displacement" and identified two underlying evolutionary mechanisms: reinforcement of reproductive barriers and "ecological displacement" (p. 59). In explaining the latter process, they wrote: "It seems clear from an *a priori* basis that any further ecological divergence lessening competition between the overlapping populations will be favoured by natural selection if it has a genetic basis (Mayr, 1949)." This is essentially a restatement of Mayr's (1949) assertion that natural selection "... tends to eliminate individuals that are closest to other sympatric species in their ecological requirements." (p. 519). Any ambiguity about what Brown & Wilson (1956) meant by ecological displacement is dispelled when they explain their concept of "competition". Referring to the definition of competition proposed by Andrewartha & Birch (1954), they wrote:

"We would adopt the part of their definition that deals with the common striving for some life requisite, such as food, space or shelter, by two or more individuals, populations or species, etc. [...] But Andrewartha and Birch, following many other writers, allow their competition concept to include another idea – that expressing direct interference of one animal or species with the life processes of another, as by fighting. On the surface, this inclusion of aggression as an element of competition might seem to some familiar and reasonable, but we wonder whether the concept of competition could be more useful in biology if it were more strictly limited to 'seeking, or endeavoring to gain, what another is endeavoring to gain at the same time', the first meaning given in *Webster's New International Dictionary* ... It is noteworthy that competition as defined by this dictionary fails to include the idea of aggression in any direct and unequivocal way.

"It may therefore be more logical in the long run to regard the various kinds of aggression between potential competitors ... as another method, parallel with character displacement and dispersion ... by which organisms seek to lessen or avoid competition." (p. 60–61)

In short, Brown & Wilson (1956) clearly did not intend ecological character displacement to include the evolution of traits involved in interference competition. For the most part, the term has continued to be used in the way that they intended. While reviews of ECD have not included character shifts caused by interspecific interference competition, it is perhaps equally telling that researchers studying such shifts have not presented their results as evidence for ECD [the sole exception that we encountered is Melville (2002)].

We think that expanding the definition of ECD to subsume the evolutionary effects of interference competition would be a mistake for at least two reasons. First, such a redefinition would result in a discontinuity between the existing literature on ECD and any future work. Existing theoretical models and reviews of ECD would logically have to be viewed as incomplete for failing to include traits used in interference competition. Second, and perhaps more important, evolutionary responses to exploitative and interference competition can involve entirely different traits and be opposite in direction.

In some cases it may be difficult, if not impossible, to determine which character displacement process is responsible for a given trait shift. For example, shifts in body size may simultaneously affect resource acquisition, mate recognition and fighting ability. This is an empirical problem, however, not a conceptual or theoretical problem. Moreover, there are certainly traits that are unlikely to be affected by exploitative competition alone (e.g. territorial signals) and others that are unlikely to be affected by interference competition (e.g. feeding adaptations), so distinguishing between different character displacement processes is not inherently intractable.

Another possible argument for expanding the definition of ECD to include evolutionary responses to interference competition is that interference mechanisms (e.g. territorial aggression) may have evolved in response to exploitative competition. We think it is conceptually clearer, however, to treat interference competition and exploitative competition as separate processes, each of which can influence the evolution of the other.