The LINNEAN SOCIETY of London BIOLOGICAL Journal of the Linnean Society

Biological Journal of the Linnean Society, 2011, **102**, 292–300. With 5 figures

Ecological character displacement in competing common green lacewings in Europe: a route to speciation?

DOMINIQUE THIERRY[1]*, MICHEL CANARD[2], BRUNO DEUTSCH[3],
MARIA A. VENTURA[4], PAULA LOURENÇO[4] and THIERRY LODÉ[5]

[1]*IRFA, Université Catholique de l'Ouest, F-49008 Angers, France*
[2]*47 Chemin Flou de Rious, F-31400 Toulouse, France*
[3]*IMA, Université Catholique de l'Ouest, F-49008 Angers, France*
[4]*CIBIO, Department of Biology, University of the Azores, Ponta Delgada, Portugal*
[5]*UMR CNRS 6552 Éthologie Évolution Écologie, Université Rennes 1, Campus de Beaulieu, F-35042 Rennes, France*

Received 11 May 2010; accepted for publication 11 August 2010

Competitive interactions among the three common green lacewing species of the *Chrysoperla* complex in Europe are presented. Four morphological characters were registered as semi-quantitative traits to assess variation between populations. Data were obtained from 325 adults originating from 14 locations. A statistical approach was performed in conjunction with observations of ecological traits and a survey of genetic relationships assessed by mitochondrial DNA cytochrome *b* analysis. The results indicate character displacement in *Chrysoperla affinis* when living in sympatry with *Chrysoperla carnea*. The morphological traits of *Ch. affinis* sympatric with *Ch. carnea* differ from those of allopatric *Ch. affinis*, although the genetic distance between those strains was weak. This was associated with a large difference in microhabitats and premating behaviour. Variation in courtship songs manifests a process of speciation within related populations. Thus, that ecological switching can also promote character displacement is supported. This suggests that character displacement acts through phenotypic variability and mediates negative interactions among species. These findings suggest that the highest rate of speciation occurs in groups of species in which competition is the strongest. © 2011 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2011, **102**, 292–300.

ADDITIONAL KEYWORDS: allopatry – *Chrysoperla* – competition – melanization – Neuroptera.

INTRODUCTION

Character displacement that changes the phenotypic expression of different co-evolving species is an expected outcome among species in overlapping distribution zones (Brown & Wilson, 1956). Morphological differences between sympatric species are driven and reinforced through interspecific competition, resulting in ecological character displacement (Servedio & Noor, 2003). Thus, the force of competition has a decisive role in promoting phenotypic divergence between interacting species.

Nonetheless, although this pattern is considered to be a key process in evolutionary ecology, few examples have been reliably documented, and several studies have consequently expressed reservation regarding this evolutionary possibility (Gerhardt, 1999). In zones of overlap, hybrids are usually intermediate between parental species in several features, such as genomic composition, ecology (Moore, 1984), and in their morphology (Berger, 1966). Species exploiting similar resources or living in sympatry are expected to have evolved in such a way as to minimize their competitive interactions. It is generally assumed that

---

*Corresponding author.
E-mail: dominique.thierry@wanadoo.fr

these species cannot coexist closely with one another (Schlutter & McPhail, 1993). Although character displacement may be a source of sympatric divergence, the importance of changes driven by natural selection and speciation remains unclear. Ecological and (/or) morphological character displacement are often presented separately without focusing on reproductive traits. Thus, it remains difficult to comment on the way in which character displacement operates. Morever, the processes leading to character specialization often stay enigmatic (Pfennig & Pfennig, 2009). An example of an ecological pattern in a complex of species belonging to the genus *Chrysoperla* (Neuroptera) is provided to demonstrate that such an evolutionary process does occur. With this model, we propose a speciation hypothesis to describe the mechanisms which occur simultaneously with ecological and morphological specialization.

The Palaearctic complex of the common green lacewings is mainly composed in Europe of three sibling species: *Chrysoperla carnea*, *Chrysoperla affinis*, and *Chrysoperla lucasina* (Tauber & Tauber, 1989). They live sympatrically, except in the Mediterranean zone where *Ch. affinis* and *Ch. carnea* reach the southern boundaries of their distribution areas and *Ch. lucasina* predominate. Nevertheless, *Ch. affinis* is abundant in certain peri-Mediterranean biotopes (Canard, Letardi & Thierry, 2007) and in the Macaronesian Islands so that *Ch. affinis* is allopatric with respect to *Ch. carnea* in those locations. Adults of *Ch. affinis* and *Ch. lucasina* are syntopic, and are found in medium and low layers of vegetation, whereas adults of *Ch. carnea* remain protected within the canopy of deciduous trees. The larvae exhibit a much stricter habitat specificity: the larvae of *Ch. lucasina* live in the low herbaceous layer, *Ch. affinis* occupies both arborescent and herbaceous layers, and the *Ch. carnea* larvae are strictly tree-inhabiting, as are the adults. The larvae of these multivoltine species develop synchronously in the vegetation as polyphagous cohorts that consume ordinary small terrestrial arthropods with soft bodies. Thus, there is strong competition between larvae.

It is expected that interspecific competition (Milbrath, Tauber & Tauber, 1993; Phoofolo & Obrycki, 1998; Mochizuchi *et al*., 2006) will reduce the niche exploitation of a species and drive ecological and morphological traits to evolve as character displacement.

MATERIAL AND METHODS

Morphological analysis of adults ($N = 325$) was conducted, taken from samples at 14 locations in Europe (Fig. 1) by hand-net sweeping in the field or in overwintering sites, under various seasonal conditions (Table 1). ‘As’ is used to refer to the strains of *Ch. affinis*’ populations living in sympatry with *Ch. carnea* (C) and ‘Aa’ for allopatric ones. All samples were divided into subsamples, each including exclusively Aa or As, or C individuals, labelled with their geographic origin. The collected specimens were immediately placed in vials filled with a standard preservative solution and stored in the dark. They were assigned to a species rank based on morphological criteria (Thierry *et al*., 1998; Henry *et al*., 2001). Morphological variation in adults was registered *sensu* Thierry, Cloupeau & Jarry (1992). Four traits were retained:

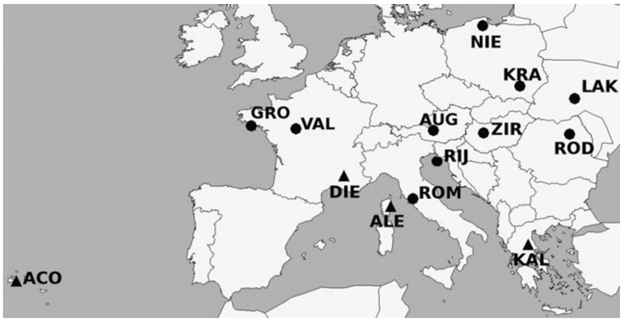

Figure 1. Sampling locations where *Chrysoperla affinis* and *Chrysoperla carnea* are sympatric and *Chrysoperla lucasina* is rare (●) and where *Ch. affinis* is allopatric and *Ch. lucasina* is dominant (▲). ACO, Azores islands; ALE, Aléria; AUG, Augsbourg; DIE, Dieulefit; GRO, Groix; KAL, Kalambáka; KRA, Krakovia; LAK, Lakatnik; NIE, Niechorze; RIJ, Rijeka; ROD, Rodna; ROM, Rome; VAL, Loire; ZIR, Zirc.

Brown mark patterns observed laterally on the stipes (ST), coded ST1 to ST4 from absent, punctiform to a mark invading the external side;

Shape of a brown mark on the genae (MG), coded MG1 to MG4 from absent to wide square mark;

Number of black setae on every side of the pronotum (PR), coded PR1 to PR4 from absent to more than 20 black setae;

Presence and distribution of black setae on the abdominal sternites (AB), coded AB1 to AB6 from absent to uniformly spread over more than 3 sternites.

A principal component analysis (PCA) of ranks was performed with all the individuals for convenient overall representation. The first principal component (FPC-PCA) was almost continuous, although there were few identical values, so it was possible to produce a suitable Tukey’s box plot to assess the relative positions of the subsamples over that variable and the geographic consistency of the

Table 1. Number of adult *Chrysoperla affinis* found sympatrically or allopatrically with *Chrysoperla carnea* during spring and summer days in 1 = deciduous arboreal vegetation outside woodlands, 2 = maize crops and canopy of lemon-trees growing in orchards, or at overwintering sites: 3 = dry bushy litter in wooded areas, 4 = barns

Community structure	Localities of sampling/coding	Date	Type of habitat	*Chrysoperla affinis*	*Chrysoperla carnea*
Sympatric	Augsbourg /AUG	17 July 2002	1	16	2
	Groix /GRO	28 April 2002	1	5	2
	Krakovie/KRA	8 July 2002	1	25	3
	Lakatnik/LAK	18 August 2002	1	25	3
	Loire valley/VAL	10 December 2000	4	42	
	Loire valley/VAL	15 December 2000	3		69
	Niechorze/NIE	29 July 2003	1	28	4
	Rodna/ROD	10 August 1999	1	20	1
	Rome/ROM	9 October 2001	3	1	13
Allopatric	Aléria/ALE	26 July 1999	1	8	
	Azores islands/ACO	10 July to 20 August 1999	2	16	
	Dieulefit/DIE	17 July 2003	1	21	
	Kalambáka/KAL	3 July 2001	1	22	

observations. Finally, the mean values of each retained character were displayed for all subsamples. A confidence interval was assigned for each mean. As the computations relied on asymptotic normality, subsamples that included more than 16 individuals were distinguished; although the degree of accuracy of these findings was not very high as a result of small sample number, it was nevertheless sufficient for further analysis. Three types of analysis were performed to increase the distinction and the strength of the character displacement. The data were not normally distributed and the homoscedasticity between subsamples could not be assumed; therefore, the small size of some subsamples required nonparametric analysis to obtain a reliable significance level. The subsamples were ordered by their mean ranks using the Kruskall–Wallis procedure. The significance level of the relative locations was determined, based on a unilateral Wilcoxon test (UWT) performed on these ranks for the two strains As and Aa and for each character. In this same way, the individuals of all subsamples were ordered according to their rank in the FPC-PCA, discriminating synthetic variables among the linear combinations of studied characters. The closest subsamples of the two strains As and Aa were identified and the individuals of those subsample were compared by a UWT. By computing the worst case, finding significant difference between the two closest subsamples should bear witness to differences between the two strains. Another way to order the subsamples is to compute confidence intervals of the character means. To proceed with statistical inference, the FCP-PCA is used, which shows a distribution property close to normal. The FCP-PCA means for subsamples whose size was greater than 16 was computed with a UWT for strains As and Aa.

Twenty-six *Chrysoperla* specimens were partially sequenced for the cytochrome *b* (cyt *b*) mitochondrial gene. Ten *Ch. affinis* and two *Ch. carnea* were collected in areas of sympatry, five *Ch. affinis* were collected in allopatric areas, and five specimens of *Ch. lucasina* were used. Outgroups (Lourenço *et al*., 2006; Haruyama *et al*., 2008) were formed by *Chrysoperla externa* (three specimens), a South American species, and *Chrysoperla rufilabris* (one specimen), a North American one. Sequences were aligned automatically based on the default parameters of CLUSTALX (Thompson *et al*., 1997). DNA polymorphism was analyzed with DNASP 4.0 (Rozas *et al*., 2003), and the MEGA 2.1 software package (Kumar *et al*., 2001) was used to calculate pairwise *p*-distances. MODELTEST 3.06 (Posada & Crandall, 1998) was used to find the best-fit model of the DNA sequence evolution. Phylogenetic relationships were inferred by maximum likelihood, maximum parsimony, and minimum evolution assuming the Jukes–Cantor substitution model for Neighbour-joining analysis. The analysis was performed using PAUP 4.0 b10 (Swofford, 2002). The final consensus tree of maximum likelihood was generated with a 50% majority rule.

In addition, larval specimen samples ($N = 209$) were obtained by sweeping the herbaceous vegetation and by beating tree branches under an umbrella in five European locations, two peri-mediterranean sites and three other western and northern sites (Table 2). Larvae were identified *in vivo*.

Table 2. The number of *Chrysoperla* larvae in herbaceous (H) and arborescent (A) vegetation

Localities of sampling	S(H)	S(A)	*Chrysoperla affinis*		*Chrysoperla carnea*		*Chrysoperla lucasina*	
			H	A	H	A	H	A
Dieulefit	30	30	0	14	0	0	12	0
Kalambáka	30	30	0	16	0	0	21	0
Krakovie	30	45	21	0	0	8	0	0
Niechorze	30	30	15	0	0	7	0	0
Loire valley	135	120	81	2	0	6	6	0

S, duration of the sampling period (min).

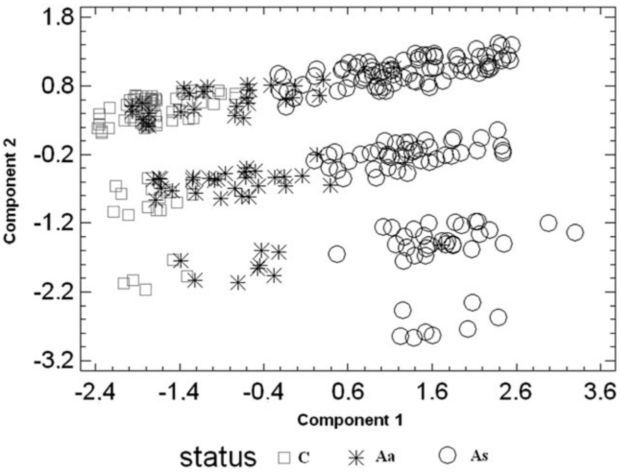

Figure 2. Scatter plot of the first two principal components. As populations of *Chrysoperla affinis* living in sympatry with *Chrysoperla carnea*; Aa, allopatric populations of *Ch. affinis*; C, *Ch. carnea.*

RESULTS

Morphological variation

The scatter plot in Figure 2 shows that *Ch. carnea* and the two strains Aa and As of *Ch. affinis* were well separated. For the characters ST, PR, and AB, the subsamples ordered by the individual mean ranks were consistently dominated by As (Table 3). On the basis of the UWT, the positions of Aa and As were significantly different ($P = 0.003$) for each character. Nevertheless, this quite robust procedure gives no information about the stability of the subsample mean ranks. The spread between the mean ranks in Aa, As, and C provides a strong likelihood of stability. Ordering by FPC- PCA leads to the same result and the robustness was supported by the Tukey's box plot (Fig. 3). Furthermore, with FPC-PCA, the closest subsamples in the mean ranks between Aa and As were Aa-ALE and As-GRO. The UWT performed on the individuals (Table 4) of these two subsamples gave a *P*-value of 0.013, confirming the high significance of the relative position of all the subsamples.

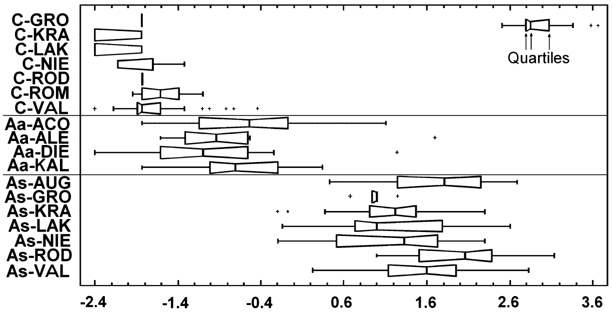

Figure 3. Tukey's box plots of first principal component for each subsample (subsamples exclusively including Aa or As, or C individuals are joined to the original locality (e.g. C-AUG or As-AUG originating from Augsbourg).

The diversity of analyses rejects, with a high level of confidence, the possibility that the relative positions of the subsamples were caused by variation within each strain of *Ch. affinis* or *Ch. carnea*, so that the translation can be assumed to apply to strain As.

Spatial distribution of larvae (Fig. 4, Table 2)

In the two peri-Mediterranean sites (Dieulefit, Kalambáka), *Ch. lucasina* was found exclusively within the herbaceous vegetation and *Ch. affinis* was found within the crowns of the trees. In the west (Loire) and north European sites (Krakovia, Niechorze), *Ch. carnea* and *Ch. affinis* were sympatric. *Ch. lucasina* seemed to reach its northern limits of repartition in Loire (only six specimens were collected) and was absent in Krakovia and Niechorze. In those sites, *Ch. carnea* was found exclusively in deciduous arborescent vegetation, whereas *Ch. affinis* then invaded the herbaceous layer.

Genetic differentiation

The molecular systematic of the *Chrysoperla carnea* complex is quite cryptic as a result of the lack of markers distinguishing the species. On the basis of

Table 3. Subsamples ordered by their mean rank of first principal component for morphological characters

PR		AB		ST		MG	
C-GRO	51	C-GRO	66	C-NIE	37	As-VAL	64
C-KRA	51	C-KRA	66	C-KRA	71	C-ROM	95
C-LAK	51	C-LAK	66	C-LAK	71	Aa-ALE	105
C-ROD	51	C-ROD	66	C-VAL	72	Aa-DIE	131
C-ROM	51	C-ROM	66	C-ROM	80	Aa-KAL	139
C-NIE	57	C-VAL	74	C-GRO	99	As-NIE	143
C-VAL	69	Aa-DIE	80	C-ROD	99	As-KRA	159
Aa-KAL	78	C-NIE	86	Aa-ACO	100	As-LAK	162
Aa-DIE	108	Aa-KAL	106	Aa-ALE	112	C-NIE	165
Aa-ALE	116	Aa-ALE	116	Aa-DIE	118	Aa-ACO	199
Aa-ACO	137	Aa-ACO	130	Aa-KAL	168	C-VAL	214
As-GRO	181	As-GRO	222	As-NIE	214	As-ROD	216
As-LAK	220	As-NIE	226	As-LAK	217	C-GRO	233
As-KRA	221	As-KRA	228	As-KRA	221	C-KRA	233
As-VAL	225	As-VAL	234	As-GRO	240	C-LAK	233
As-NIE	227	As-LAK	241	As-VAL	240	C-ROD	233
As-AUG	260	As-AUG	275	As-AUG	246	As-AUG	233
As-ROD	263	As-ROD	284	As-ROD	260	As-GRO	233
$P = 0.003$		$P = 0.003$		$P = 0.003$		$P = 0.11$	

ST, brown mark patterns observed laterally on the stipes; MG, shape of a brown mark on the genae; PR, number of black setae on every side of the pronotum; AB, presence and distribution of black setae on the abdominal sternites. The rounded values are based on the Wilcoxon test. For localities, see Table 1.

Table 4. Individuals of the closest subsamples of strains As and Aa ordered according to the values of the first principal component (FPC)

Individuals	FPC
Aa-ALE	–1.61
Aa-ALE	–1.32
Aa-ALE	–1.30
Aa-ALE	–1.10
Aa-ALE	–0.79
Aa-ALE	–0.58
Aa-ALE	–0.53
As-GRO	0.68
As-GRO	0.94
As-GRO	0.99
As-GRO	0.99
As-GRO	1.25
Aa-ALE	1.70
$P = 0.013$	

For localities, see Table 1.

Cyt *b* (Fig. 5), sympatric *Ch. affinis* As was in a well-separated cluster, and quite different from allopatric individuals Aa. The molecular relationships between *Ch. lucasina*, *Ch. carnea*, and *Ch. affinis* (Aa) were not yet well defined. *Ch. lucasina* appeared in a cluster that was only weakly differentiated from *Ch. carnea* and *Ch. affinis* Aa.

Nucleotide sequences have been deposited in the GenBank database (accession numbers AY743861 to AY743863, AY743865, AY743866, AY743868, AY743872, AY743874, AY743878, AY743882 to AY743885, AY743889 to AY743893, AY743899, and AY743902 to AY743908).

DISCUSSION

Variation in morphological traits, ecological shift, and pre-zygotic divergence in courtship calls were manifested, otherwise there is a weak genetic difference between populations. This emphasizes that hard competition may heavily affect these traits.

MORPHOLOGICAL CHARACTERIZATION

The evolutionary impact of competition upon morphological traits and co-evolution has already been extensively debated (Taper & Case, 1992), although not deeply investigated. Because mechanisms should also primarily result in phenotypic changes, pairs of new species of a similar size tend not to co-occur syntopically, suggesting that competitive interactions could prevent their coexistence (Buskirk, 2007). The morphological patterns exhibited by common green lacewings were consistent with a co-evolution response resulting from competitive interactions. The populations of *Ch. affinis* sympatric with *Ch. carnea* were significantly different morphologically from popula-

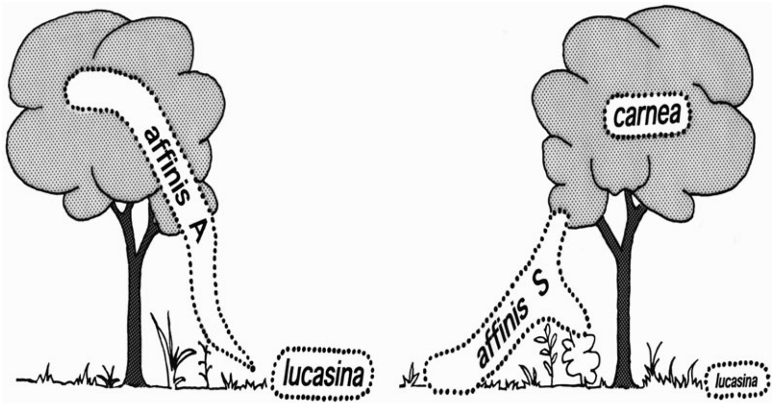

Figure 4. Distribution of the larvae of European green lacewings in the peri-Mediterranean area where *Chrysoperla affinis* (A) is allopatric with *Chrysoperla carnea* and in the sympatric area between *Ch. affinis* (S) and *Ch. carnea*.

tions of allopatric *Ch. affinis*. They showed increased melanization by black silks and the extension of dark marks on the exoskeleton. Such chromatic variation could be linked to the habitat, although a comparison between randomly paired allopatric populations of *Ch. affinis* did not reveal continuous or even semi-continuous distribution in the geographic range or along a pattern of resource availability. Although resource distribution was the same in sympatry and allopatry, *Ch. affinis* did not exhibit this morphological trait anywhere in the allopatric areas. Therefore, character variation does not simply reflect differences in resource availability and thus suggests that *Ch. affinis* populations have evolved separately. Moreover, morphological character displacement only occurred in the sympatric populations when *Ch. affinis* overlapped with *Ch. carnea*. Although ecological character displacement is the main explanation for morphological changes, some environmental conditions may require variation as adjustments to peculiar habitats (Goldberg & Lande, 2006). Nevertheless, the heritability of morphological changes in *Ch. affinis* is observed in adults from similar breeding lineages (Thierry *et al*., 1992).

ECOLOGICAL SHIFT

Morphological character displacement in *Ch. affinis* was associated with some peculiar habitat features, revealing an ecological shift. Indeed, changes are driven through interplay between inter- and intraspecific competition (Brown & Wilson, 1956) and linked to the exploitation of different resources. In *Chrysoperla* species, reproduction and pre-imaginal stages are committed to a particular layer of vegetation where glyco-palyniphagous adults feed on a narrow range of pollen (Villenave *et al*., 2006). In the peri-Mediterranean zone, the larvae of *Ch. affinis* chiefly dwell in trees, whereas those of *Ch. lucasina* are found exclusively in the herbaceous layer. In its northwestern range, *Ch. affinis* overlaps *Ch. carnea*, which is entirely dependent on trees. Their competitive interactions resulted in exploitation of new habitats, with the exclusion of *Ch. affinis* from the trees and its restriction to the low layer. Such a translocation was facilitated because the thermophilous *Ch. lucasina* reached the limits of its northern range. Resource competition is recognized as a major condition for character displacement (Losos, 2000). It may result from competition with *Ch. carnea* for limited food resources for both adults and larvae. Competitive interactions may also prevent aggressive behavioural interferences, which could be a factor in the ecological shift as reported in the damselfly *Calopteryx* (Tynkkynen, Rantala & Suhoneon, 2004). Although ‘Gloger’s rule’ is most applicable to vertebrates (Lodé, 2001), a similar mechanism may be involved. *Ch. affinis* oviposition and development is mainly restricted to the herbaceous stratum (i.e. a dark wet habitat with little ventilation where dark coloured marks on the exoskeleton may have a certain adaptive value and a significant role in strong competitive interactions, such as cannibalism and intraguild predation) (Mochizuchi *et al*., 2006). It is already known that some species of *Chrysoperla* are cryptically coloured in their own habitat as a result of strong selection by vertebrate predators (Tauber & Tauber, 1987).

GENETIC DIFFERENTIATION VERSUS DIVERGENCE IN COURTSHIP CALLS

Because character displacement results from a selection against maladaptive hybridization, such an ecological shift has been hypothesized as a powerful source of genetic differentiation (Radtkey, Fallon & Case, 1997). The existence of some rare morphologically intermediate individuals suggests that the

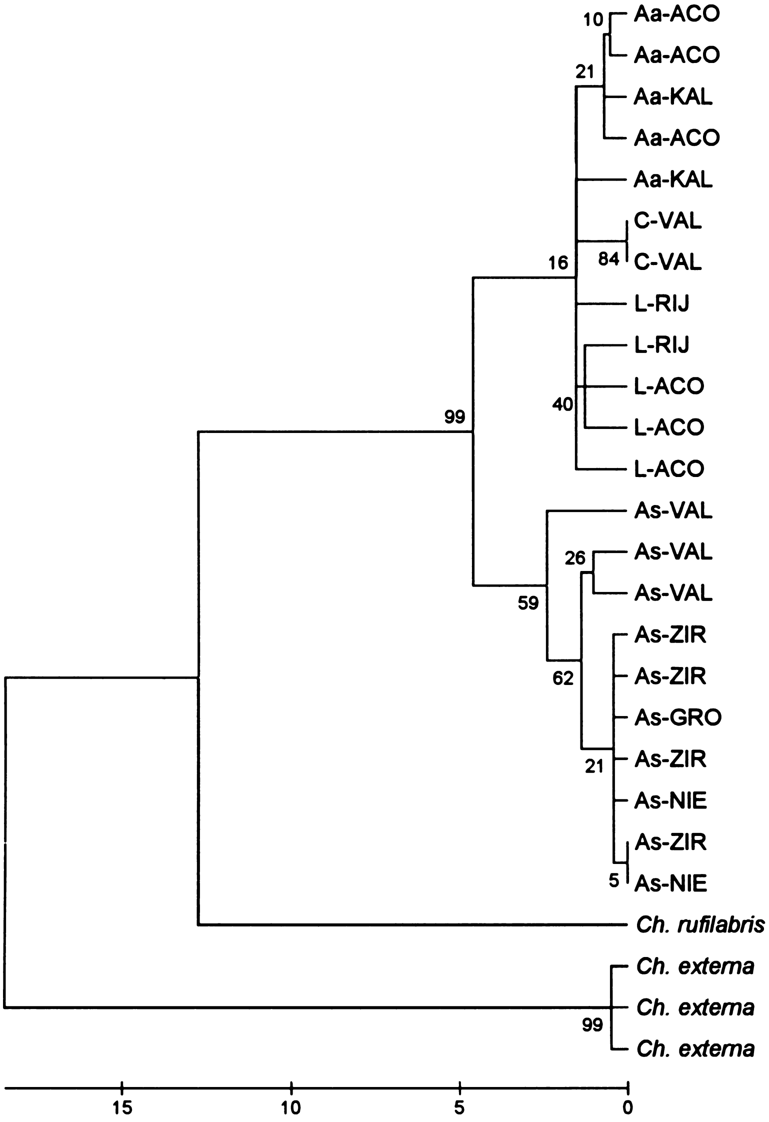

Figure 5. Bootstrap consensus tree obtained from DNA sequences of the cytochrome *b* mitochondrial gene inferred by maximum likelihood. Each individual sampled in Europe is designated by its population type: *Chrysoperla affinis* (As) living in sympatry with *Chrysoperla carnea* (C), allopatric populations of *Ch. affinis* (Aa), *Chrysoperla lucasina* (L).

hybridization of *Ch. affinis* may occur in sympatric areas (Thierry, Cloupeau & Jarry, 1994). Sympatric populations of *Ch. affinis*, however, exhibit a clear genetic differentiation from allopatric ones. Although systematic positioning of these populations was not precise, the genetic differentiation associated with a drastic ecological shift suggests that a specific deviation occurred.

Diversification in common green lacewings involves changes in the substrate-borne songs that males and females produce during courtship (Henry & Wells, 2004). *Chrysoperla lucasina* exhibited a very particular courtship call, whereas *Ch. carnea* and *Ch. affinis* have relatively close calls. Nevertheless, the morphological and genetic differentiation between *Ch. affinis* living sympatrically with *Ch. carnea* and allopatric populations of *Ch. affinis* is associated with differences in courtship calls (Henry *et al.*, 2001). The variation in calls appears consistent with a process of reinforcement that increases the pre-zygotic reproductive isolation between recently diverged strains (Coyne & Orr, 1989, 1997; Servedio & Noor, 2003). Divergences in the pattern of mating preference lead to reproductive character reinforcement (Sætre *et al.*, 1997; Albert, Millar & Schluter, 2007; Mullen & Andrés, 2007). Pre-zygotic mechanisms of the specific mate recognition system (SMRS) predominate in the speciation process, whereas post-zygotic and genetic differentiations occur later. In this case, it is questionable to what degree the courtship songs function as barriers to hybridization in the field (Tauber & Tauber, 1989), although they appear to be related to an ecological shift and may reinforce the genetic divergence between habitat-diversified populations. A classic pattern of character displacement is less likely to occur for a trait that affects resource acquisition than for a trait that affects mate choice (Goldberg & Lande, 2006). Indeed, changes in SMRS could have a crucial role in evolutionary biology because signals and responses may promote reproductive isolation among populations (Paterson, 1985) and could therefore result in the formation of new species (Marshall & Cooley, 2000; Höbel & Gerhardt, 2003).

CONCLUSIONS

The original combination of competitive interactions between European common green lacewings showed evidence of character displacement, as revealed by morphological traits, an ecological shift, and changes in the pre-mating system. Five outcomes elaborated by Taper & Case (1992) led to the competition hypothesis for character displacement and reinforcement: (1) a link between repartition and morphological phenotypic divergence; (2) a habitat switch for new resources, indicating resource/habitat competition; (3) a major difference between the sites as a result of the presence or absence of competing species; (4) phenotypic differences; and (5) a process of genetic differentiation and pre-zygotic isolation because the courtship calls differed among taxa.

Divergent selection as a result of competition could explain why closely-related coexisting species typically differ in phenotype and why the degree of character displacement reflects the intensity of competition between interacting species (Pfennig & Murphy, 2002). The context is different from particular environmental situations in which clear-cut examples of character displacement have been reported, such as in host races (Feder *et al*., 2003). The common green lacewing guild inhabits a trivial environment where a community of species shares an assemblage of available niches, a situation commonly found in terrestrial biocenoses of the western Palearctic. It could be argued that the selection of characters needed for survival occurred before the reproductive character displacement, and that SMRS changes act as a reinforcement, emphasizing the importance of conflict among coexisting species. Thus, based on the hypothesis that phenotypic specialization preceded specific differentiation, the displacement of ecological characters was first required for survival in a context of severe competition (Lodé, 2006). Selection against hybridization has actually acted to lessen gene flow and to promote speciation. The cryptic common green lacewings may provide a clear example of competition based on divergence both in premating signals and in morphological, ecological, and genetic traits, resulting in a speciation process, a situation that is undoubtedly common in nature. Selection to lessen ecological competition can drive character displacement, suggesting that such an event acts through phenotypic variability and may mediate negative interactions among species. These results suggest that groups of species in which the competition is the strongest are likely to exhibit the highest rate of speciation.

ACKNOWLEDGEMENTS

We thank two anonymous referees for their advice, especially the second referee for the fine correction of the paper, as well as A. E. Whittington (Edinburgh, Scotland, UK) who assisted with linguistic improvement.

REFERENCES

Albert AYK, Millar NP, Schluter D. 2007. Character displacement of male nuptial colour in threespine sticklebacks. *Biological Journal of the Linnean Society* **91:** 37–48.

Berger L. 1966. Biometrical studies on the population of green frogs from the environs of Poznan. *Annals of Zoology* **23:** 303–324.

Brown WL, Wilson EO. 1956. Character displacement. *Systematic Zoology* **5:** 49–64.

Buskirk JV. 2007. Body size, competitive interactions, and the local distribution of *Triturus* newts. *Journal of Animal Ecology* **76:** 559–567.

Canard M, Letardi A, Thierry D. 2007. The rare Chrysopidae of southwestern Europe. *Acta Oecologia* **31:** 290–298.

Coyne JA, Orr HA. 1989. Pattern of speciation in Drosophila. *Evolution* **43:** 362–381.

Coyne JA, Orr HA. 1997. Pattern of speciation in *Drosophila* revisited. *Evolution* **51:** 295–303.

Feder JL, Berlocher SH, Roethele JB, Dambroski HR, Smith JJ, Perry WL, Gavrilovic V, Filchak KE, Rull J, Aluja M. 2003. Allopatric genetic origins for sympatric hostplant shifts and race formation in *Rhagoletis*. *Proceedings of the National Academy of Sciences of the United States of America* **100:** 10314–10319.

Gerhardt HC. 1999. Reproductive character displacement and other sources of environmental selection on acoustic communication systems. In: Hauser M, Konishi M, eds. *The design of animal communication*. Cambridge, MA: MIT Press, 515–534.

Goldberg EE, Lande R. 2006. Ecological and reproductive character displacement on an environmental gradient. *Evolution* **60:** 1344–1357.

Haruyama N, Mochizuki A, Duelli P, Naka H, Nomora M. 2008. Green lacewing phylogeny, based on three nuclear genes. *Systematic Entomology* **33:** 275–288.

Henry CS, Wells MLM. 2004. Adaptation or random change? The evolutionary response of songs to substrate properties in lacewings. *Animal Behaviour* **68:** 879–895.

Henry CS, Brooks SJ, Thierry D, Duelli P, Johnson JB. 2001. The common green lacewing *(Chrysoperla carnea s. lat.)* and the sibling species problem. In: McEwen PK, New TR, Whittington AE, eds. *Lacewings in the crop environment*. Cambridge: Cambridge University Press, 29–42.

Höbel G, Gerhardt HC. 2003. Reproductive character displacement in the acoustic communication system of green tree frogs (*Hyla cinerea*). *Evolution* **57:** 894–904.

Kumar S, Tamura K, Jakobsen IB, Nei M. 2001. MEGA2: molecular evolutionary genetics analysis software. *Bioinformatics* **17:** 1244–1245.

Lodé T. 2001. Genetic divergence without spatial isolation in polecat *Mustela putorius* populations. *Journal of Evolutionary Biology* **14:** 228–236.

Lodé T. 2006. *The war of the sexes in the animals. A natural history of sexuality*. Paris: Odile Jacob Publ. (in French).

Losos JB. 2000. Ecological character displacement and the study of adaptation. *Proceedings of the National Academy of Sciences of the United States of America* **97:** 5693–5695.

Lourenço P, Brito C, Backeljau T, Thierry D, Ventura MA. 2006. Molecular systematic of *Chrysoperla carnea* group in Europe. *Journal of Zoological Systematics and Evolutionary Research* **44:** 180–184.

Marshall DC, Cooley JR. 2000. Reproductive character displacement and speciation in periodical cicadas, with description of a new species. *Evolution* **54:** 1313–1325.

Milbrath LR, Tauber MJ, Tauber C. 1993. Prey specificity in *Chrysopa*: an interspecific comparison of larval feeding and defensive behavior. *Ecology* **74:** 1384–1393.

Mochizuchi A, Naka H, Hamasaki K, Mitsunaga T. 2006. Larval cannibalism and intraguild predation between the introduced green lacewing and the indigenous trash-carrying green lacewing. *Environmental Entomology* **35:** 1298–1303.

Moore WS. 1984. Evolutionary ecology of uni-sexual fishes. In: Turner BJ, ed. *Evolutionary genetics of fishes*. New York, NY: Plenum Press, 329–398.

Mullen SP, Andrés JA. 2007. Rapid evolution of sexual signals in sympatric *Calopteryx* damselflies: reinforcement or 'noisy-neighbour' ecological character displacement. *Journal of Evolutionary Biology* **20:** 637–1648.

Paterson HEH. 1985. The recognition species concept. In: Vrba E, ed. *Species and speciation*. Pretoria: Transvaal Museum Monograph, 21–29.

Pfennig DW, Murphy PJ. 2002. How fluctuating competition and phenotypic plasticity mediate species divergence. *Evolution* **56:** 1217–1228.

Pfennig KS, Pfennig DW. 2009. Character displacement: ecological and reproductive response to a common evolutionary problem. *Quarterly Review of Biology* **8:** 253–276.

Phoofolo MW, Obrycki JJ. 1998. Potential for intraguild predation and competition among predatory Coccinellidae and Chrysopidae. *Entomologia Experimentalis et Applicata* **89:** 47–55.

Posada D, Crandall A. 1998. Modeltest: testing the model of DNA substitution. *Bioinformatics* **14:** 817–818.

Radtkey RR, Fallon SM, Case TJ. 1997. Character displacement in some *Cnemidophorus* lizards revisited: a phylogenetic analysis. *Proceedings of the National Academy of Sciences of the United States of America* **94:** 9740–9745.

Rozas J, Sanchez-DelBarrio JC, Messeguer X, Rozas R. 2003. DnaSP, DNA polymorphism analyses by the coalescent and other methods. *Bioinformatics* **19:** 2496–2497.

Sætre GP, Moum T, Bures S, Kral M, Adamjan M, Moreno J. 1997. A sexually selected character displacement in flycatchers reinforces premating isolation. *Nature* **387:** 589–592.

Schlutter D, McPhail JD. 1993. Character displacement and replicate adaptive radiation. *Trends in Ecology & Evolution* **8:** 197–200.

Servedio MR, Noor MAF. 2003. The role of reinforcement in speciation: theory and data. *Annual Review of Ecology and Systematics* **34:** 339–364.

Swofford DL. 2002. *PAUP: phylogenetic analysis using parsimony (and other methods)*, Version 4.0. User's manual. Sunderland, MA: Sinauer Associates.

Taper ML, Case TJ. 1992. Models of character displacement and the theoretical robustness of taxon cycles. *Evolution* **46:** 317–333.

Tauber CA, Tauber MJ. 1987. Insect seasonal cycles: genetics and evolution. *Annual Review of Ecology and Systematics* **12:** 281–308.

Tauber CA, Tauber MJ. 1989. Sympatric speciation in insects: perception and perspective. In: Otte D, Endler JA, eds. *Speciation and its consequences*. Sunderland, MA: Sinauer Associates, 307–344.

Thierry D, Cloupeau R, Jarry M. 1992. La Chrysope commune *Chrysoperla carnea* (Stephens) sensu lat dans le centre de la France: mise en evidence d'un complexe d'especes (Insecta: Neuroptera: Chrysopidae). In: Canard M, Aspock H, Mansell MW, eds. *Current Research in Neuropterology. Proceedings of the Fourth International Symposium on Neuropterology*. Toulouse: Sacco, 379–392.

Thierry D, Cloupeau R, Jarry M. 1994. Variation in the overwintering ecophysiological traits in the common green lacewing west-Palaearctic complex. *Acta Oecologia* **15:** 593–606.

Thierry D, Cloupeau R, Jarry M, Canard M. 1998. Discrimination of the West-Palaearctic species of the *carnea* group by means of claw morphology. *Acta Zoologica Fenica* **209:** 255–262.

Thompson JD, Gibson TJ, Plewniak F, Jeanmougin F, Higgins D-G. 1997. The ClustalX windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Research* **25:** 4876–4882.

Tynkkynen K, Rantala MJ, Suhoneon J. 2004. Interspecific aggression and character displacement in the damselfly *Calopteryx splendens*. *Journal of Evolutionary Biology* **17:** 759–767.

Villenave J, Deutsch B, Lodé T, Rat-Morris E. 2006. Pollen preference of the *Chrysoperla* species occurring in the crop environment. *European Journal of Entomology* **103:** 771–777.