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(AB=("reproductive barriers" OR "reproductive isolation") OR AK=("reproductive barriers" OR "reproductive isolation") OR TI=("reproductive barriers" OR "reproductive isolation")) AND (ALL=(Odonata))

23/05/2022

REVISION OF THE PUELLA GROUP OF THE GENUS COENAGRION KIRBY, 1890 (ODONATA, ZYGOPTERA), WITH EMPHASIS ON MORPHOLOGIES CONTRIBUTING TO REPRODUCTIVE ISOLATION

BATTIN, TJ. 1993

The puella group of the zygopteran genus Coenagrion Kirby, 1890 is revised. The group, as treated here, includes C. puella (L., 1758), C. syriacum (Morton, 1924), C. ponticum (Bartenef, 1929) and C. intermedium (Lohmann, 1990). All four species are redescribed on the basis of a scanning electron microscopical (S.E.M.) analysis of morphological characters involved in copulation. Full species rank is attributed to intermedium. A key to males and females of the four species is included. Reproductive isolation is discussed in the genus Coenagrion.

HYBRIDIZATION BETWEEN 2 DAMSELFLY SPECIES (ODONATA, COENAGRIONIDAE) - MORPHOMETRIC AND GENITALIC DIFFERENTIATION

LEONG, JM; HAFERNIK, JE. 1992

In allopatry and in a **hybrid** zone, we analyzed the relationship between morphometric characters and the inferior abdominal appendage angle in two damselflies, Ischnura gemina (Kennedy) and Ischnura denticollis (Burmeister), to assess the taxonomic reliability and genetic basis of this genitalic trait. Changes in the morphometric-genitalic relationship in the **hybrid** zone strongly imply that introgression has occurred, although there is some evidence of **hybrid** unfitness and partial reproductive isolation. We conclude that the inferior appendage trait is not taxonomically reliable because it fails to convey the recombinant nature of individuals in the **hybrid** zone. A combination of field and lab data suggest that the genitalic angle trait is polygenic but controlled by only a few genes. We argue for retention of full species status for both I. gemina and I. denticollis, despite genetic exchange between the two.

Hybridization between Ischnura graellsii (Vander Linder) and I-elegans (Rambur) (Odonata : Coenagrionidae): are they different species?

Monetti, L; Sanchez-Guillen, RA; Rivera, AC. 2002

Two closely related damselflies, Ischnura graellsii and I. elegans, were analysed for morphological differences and reproductive isolation in the north coast of Galicia (NW Spain). We compared animals from sympatric and allopatric localities, including I. elegans from Belgium and I. graellsii from southern Spain as pure allopatric populations. A set of morphometric characters were studied by means of multivariate discriminant analysis to determine if these two species can be unambiguously distinguished. Discriminant analysis revealed that I. graellsii and I. elegans are well differentiated on the first two axis (86% and 11%, respectively). I. graellsii individuals are distinguished from I. elegans by their smaller size and, specifically, by their narrower and shorter wings and shorter tibiae. In addition, I. elegans has a narrower space between the branches of each cercus, and greater distance between the branches of each paraproct. Sympatric individuals are morphologically intermediate, suggesting **hybrid**ization. When the species were put together in the laboratory, they showed partial temporal separation in mating behaviour, but males of I. elegans readily mated with females of I. graellsii, and **hybrid** individuals were obtained. The opposite heterospecific cross was almost impossible, apparently because of mechanical problems with the tandem linkage. Laboratory-reared **hybrid**s (from male I. elegans x female I. graellsii) are morphologically intermediate, mainly resembling the maternal phenotype. Although **hybrid**ization between both taxa is common, we suggest maintaining the specific status for both phenotypes because they show incipient reproductive isolation, as it is reported in the literature. (C) 2002 The Linnean Society of London, Biological Journal of the Linnean Society, 2002, 76, 225-235.

Biogeography and systematics of endemic island damselflies: The Nesobasis and Melanesobasis (Odonata: Zygoptera) of Fiji

Beatty, CD; Herrera, MS; Skevington, JH; Rashed, A; Van Gossum, H; Kelso, S; Sherratt, TN. 2017

The study of island fauna has greatly informed our understanding of the evolution of diversity. We here examine the phylogenetics, biogeography, and diversification of the damselfly genera Nesobasis and Melanesobasis, endemic to the Fiji Islands, to explore mechanisms of speciation in these highly speciose groups. Using mitochondrial (COI, 12S) and nuclear (ITS) replicons, we recovered Garli-part maximum likelihood and Mrbayes Bayesian phylogenetic hypotheses for 26 species of Nesobasis and eight species/subspecies of Melanesobasis. Biogeographical patterns were explored using Lagrange and Bayes-Lagrange and interpreted through beast relaxed clock dating analyses. We found that Nesobasis and Melanesobasis have radiated throughout Fiji, but are not sister groups. For Nesobasis, while the two largest islands of the archipelagoViti Levu and Vanua Levucurrently host two distinct species assemblages, they do not represent phylogenetic clades; of the three major groupings each contains some Viti Levu and some Vanua Levu species, suggesting independent colonization events across the archipelago. Our Beast analysis suggests a high level of species diversification around 2-6Ma. Our ancestral area reconstruction (Rasp-Lagrange) suggests that both dispersal and vicariance events contributed to the evolution of diversity. We thus conclude that the evolutionary history of Nesobasis and Melanesobasis is complex; while inter-island dispersal followed by speciation (i.e., peripatry) has contributed to diversity, speciation within islands appears to have taken place a number of times as well. This speciation has taken place relatively recently and appears to be driven more by reproductive isolation than by ecological differentiation: while species in Nesobasis are morphologically distinct from one another, they are ecologically very similar, and currently are found to exist sympatrically throughout the islands on which they are distributed. We consider the potential for allopatric speciation within islands, as well as the influence of parasitic endosymbionts, to explain the high rates of speciation in these damselflies.

Rapid evolution of prezygotic barriers in non-territorial damselflies

Sanchez-Guillen, RA; Cordoba-Aguilar, A; Cordero-Rivera, A; Wellenreuther, M. 2014

A central question in evolutionary biology concerns the accumulation of reproductive barriers during speciation. However, separating the reproductive barriers that have led to speciation from those that have secondarily accumulated (i.e. after initial divergence) is a widely recognized problem. Ideal candidate species for overcoming this problem are young species, where time for additional barriers to accrue has been limited. In the present study, we add to previous studies investigating the strength of reproductive barriers between the parapatric damselflies Ischnura elegans and Ischnura graellsii by quantifying seven prezygotic barriers between the allopatric pairs of I.elegans and Ischnura genei, as well as I.graellsii and I.genei. Specifically, we measured four premating (temporal, sexual, mechanical (I), and mechanical (II)) and three postmating (oviposition success, fecundity, and fertility) barriers using experimental approaches and, for first time, we investigated the mechanisms causing mechanical isolation, which is the strongest reproductive barrier in ischnurans. The findings of the present study support the notion that premating barriers are generally strong and contribute significantly to total reproductive isolation in young lineages (65-98%), although they never solely lead to complete isolation. Asymmetry was generally stronger in premating than in postmating barriers, and was driven mostly through asymmetry in mechanical isolation, which is caused by morphological divergence of secondary sexual appendages. We found that barriers act multiplicatively in all species combinations tested, with the exception of sexual isolation, which was not detected. Our results are consistent with a recent allopatric speciation scenario driven by differences in male anal

appendages, either impeding copulation or affecting female preferences. Taken together, the results from this and previous studies in diverse odonate genera suggest that premating barriers have evolved rapidly in ischnuran damselflies and, although reproductive isolation in ischnurans is more commonly the result of several barriers acting together, morphological divergence of secondary sexual appendages appears to be a common factor facilitating premating isolation in this group.(c) 2014 The Linnean Society of London, Biological Journal of the Linnean Society, 2014, 113, 485-496.

Mechanical and tactile incompatibilities cause reproductive isolation between two young damselfly species

Barnard, AA; Fincke, OM; McPeek, MA; Masly, JP. 2017

External male reproductive structures have received considerable attention as a cause of reproductive isolation (RI), because the morphology of these structures often evolves rapidly between populations. This rapid evolution presents the potential for mechanical incompatibilities with heterospecific female structures during mating and could thus prevent interbreeding between nascent species. Although such mechanical incompatibilities have received little empirical support as a common cause of RI, the potential for mismatch of reproductive structures to cause RI due to incompatible species-specific tactile cues has not been tested. We tested the importance of mechanical and tactile incompatibilities in RI between Enallagma anna and E. carunculatum, two damselfly species that diverged within the past similar to 250,000 years and currently **hybrid**ize in a sympatric region. We quantified 19 prezygotic and postzygotic RI barriers using both naturally occurring and laboratory-reared damselflies. We found incomplete mechanical isolation between the two pure species and between **hybrid** males and pure species females. Interestingly, in mating pairs for which mechanical isolation was incomplete, females showed greater resistance and refusal to mate with **hybrid** or heterospecific males compared to conspecific males. This observation suggests that tactile incompatibilities involving male reproductive structures can influence female mating decisions and form a strong barrier to gene flow in early stages of speciation.

STRONG ASYMMETRY IN THE RELATIVE STRENGTHS OF PREZYGOTIC AND POSTZYGOTIC BARRIERS BETWEEN TWO DAMSELFLY SISTER SPECIES

Sanchez-Guillen, RA; Wullenreuther, M; Rivera, AC. 2012

One of the longest debates in biology has been over the relative importance of different isolating barriers in speciation. However, for most species, there are few data evaluating their relative contributions and we can only speculate on the general roles of pre- and postzygotic isolation. Here, we quantify the absolute and cumulative contribution of 19 potential reproductive barriers between two sympatric damselfly sister species, Ischnura elegans and I. graellsii, including both premating (habitat, temporal, sexual and mechanical isolation) and postmating barriers (prezygotic: sperm insemination success and removal rate, oviposition success, fertility, fecundity; postzygotic: **hybrid** viability, **hybrid** sterility and **hybrid** breakdown). In sympatry, total reproductive isolation between I. elegans females and I. graellsii males was 95.2%, owing mostly to a premating mechanical incompatibility (93.4%), whereas other barriers were of little importance. Isolation between I. graellsii females and I. elegans males was also nearly complete (95.8%), which was caused by the cumulative action of multiple prezygotic (n= 4, 75.4%) and postzygotic postmating barriers (n= 5, 7.4%). Our results suggest that premating barriers are key factors in preventing gene flow between species, and that the relative strengths of premating barriers is highly asymmetrical between the reciprocal crosses.

Widespread Wolbachia infection in an insular radiation of damselflies (Odonata, Coenagrionidae)

Lorenzo-Carballa, MO; Torres-Cambas, Y; Heaton, K; Hurst, GDD; Charlat, S; Sherratt, TN; Van Gossum, H; Cordero-Rivera, A; Beatty, CD. 2019

Wolbachia is one of the most common endosymbionts found infecting arthropods. Theory predicts symbionts like Wolbachia will be more common in species radiations, as host shift events occur with greatest frequency between closely related species. Further, the presence of Wolbachia itself may engender reproductive isolation, and promote speciation of their hosts. Here we screened 178 individuals belonging to 30 species of the damselfly genera Nesobasis and Melanesobasis - species radiations endemic to the Fiji archipelago in the South Pacific - for Wolbachia, using multilocus sequence typing to characterize bacterial strains. Incidence of Wolbachia was 71% in Nesobasis and 40% in Melanesobasis, and prevalence was also high, with an average of 88% in the Nesobasis species screened. We identified a total of 25 Wolbachia strains, belonging to supergroups A, B and F, with some epidemic strains present in multiple species. The occurrence of Wolbachia in both males and females, and the similar global prevalence found in both sexes rules out any strong effect of Wolbachia on the primary sex-ratio, but are compatible with the phenotype of cytoplasmic incompatibility. Nesobasis has higher species richness than most endemic island damselfly genera, and we discuss the potential for endosymbiont-mediated speciation within this group.

Complex evolutionary history of the American Rubyspot damselfly, Hetaerina americana (Odonata): Evidence of cryptic speciation

Vega-Sanchez, YM; Mendoza-Cuenca, LF; Gonzalez-Rodriguez, A. 2019

Analyzing the magnitude and distribution of genetic variation within and among populations allows for hypothesis testing about historical demographic size changes, secondary contacts, refugia, and speciation patterns. Species distribution and genetic structure are greatly influenced by the complex life cycle and behavior of odonates. Hetaerina americana has been widely used as a model system in behavioral studies, but its population genetic structure has not been analyzed, except for a single study that included only three populations but identified the presence of markedly differentiated genetic groups, suggesting the existence of cryptic species. Here, we tested this hypothesis by assessing throughout the distribution range of H. americana the patterns of genetic and morphological variation in the male caudal appendages, due to the great importance of these structures in mate recognition. As molecular markers we used sequences of the mitochondrial cytochrome oxidase I (COI) gene and the nuclear internal transcribed spacer (ITS) region, as well as six nuclear micro-satellites. We found very high population genetic differentiation (Phi(ST) > 0.51) in the three sets of markers but with strong mitonuclear discordance. A neutrality test suggested that the mitochondrial genome might be under purifying selection in association to climatic variables (temperature seasonality). The assignment of individuals to nuclear genetic groups showed little admixture and complete congruence with morphological differentiation in the male caudal appendages. Hence, the results suggest that H. americana represents at least two different cryptic species which are isolated reproductively.

Postmating sexual selection: Allopatric evolution of sperm competition mechanisms and genital morphology in calopterygid damselflies (Insecta : Odonata)

Rivera, AC; Andres, JA; Cordoba-Aguilar, A; Utzeri, C. 2004

Postmating sexual selection theory predicts that in allopatry reproductive traits diverge rapidly and that the resulting differentiation in these traits may lead to restrictions to gene flow between populations and, eventually, reproductive isolation. In this paper we explore the potential for this premise in a group of damselflies of the family Calopterygidae, in which postmating sexual mechanisms are especially well understood. Particularly, we tested if in allopatric populations the sperm competition mechanisms and genitalic traits involved in these mechanisms have indeed diverged as sexual selection theory predicts. We did so in two different steps. First, we compared the sperm competition mechanisms of two allopatric populations of Calopteryx haemorrhoidalis (one Italian population studied here and one Spanish population previously studied). Our results indicate that in both populations males are able to displace spermathecal sperm, but the mechanism used for sperm removal between both populations is strikingly different. In the Spanish population males seem to empty the spermathecae by stimulating females, whereas in the Italian population males physically remove sperm from the spermathecae. Both populations also exhibit differences in genital morphometry that explain the use of different mechanisms: the male lateral processes are narrower than the spermathecal ducts in the Italian population, which is the reverse in the Spanish

population. The estimated degree of phenotypic differentiation between these populations based on the genitalic traits involved in sperm removal was much greater than the differentiation based on a set of other seven morphological variables, suggesting that strong directional postmating sexual selection is indeed the main evolutionary force behind the reproductive differentiation between the studied populations. In a second step, we examined if a similar pattern in genital morphometry emerge in allopatric populations of this and other three species of the same family (Calopteryx splendens, C. virgo and Hetaerina cruentata). Our results suggest that there is geographic variation in the sperm competition mechanisms in all four studied species. Furthermore, genitalic morphology was significantly divergent between populations within species even when different populations were using the same copulatory mechanism. These results can be explained by probable local coadaptation processes that have given rise to an ability or inability to reach and displace spermathecal sperm in different populations. This set of results provides the first direct evidence of intraspecific evolution of genitalic traits shaped by postmating sexual selection.

DENSITY-DEPENDENT MATING SUCCESS AND COLOR POLYMORPHISM IN FEMALES OF THE DAMSELFLY ISCHNURA-GRAELLSII (ODONATA, COENAGRIONIDAE)

CORDERO, A. 1992

1. Female-limited colour polymorphism is very common in odonates. One of the forms has male-like colouring (androchromotypics), while the other(s) is cryptic (gynochromotypics). Three hypotheses have been proposed to explain the maintenance of this polymorphism: (1) higher reproductive isolation of androchromotypics, balanced by higher predation on this form; (2) androchromotypics avoid unnecessary long matings, but suffer greater predation; and (3) androchromotypics avoid male harassment at high density, but have lower mating success at low density. 2. To test these hypotheses I measured survivorship and mating success of andro- and gynochromotypic females of Ischnura graellsii in two natural populations with different densities in Galicia (NW Spain). 3. Contrary to the predictions of hypotheses 1 and 2, mean longevity and daily survival rate was the same for andro- and gynochromotypics. 4. Mating success was the same for andro- and gynochromotypics at high density but the proportion of unmated females was greater in andro- than gynochromotypics at low density. Furthermore, androchromotypics mated with longer inter-copula intervals at high density, and mating duration was also density-dependent. These results suggest that hypothesis 3 is the most appropriate to explain the maintenance of the polymorphism. 5. Androchromotypics were larger than gynochromotypics in the high density population. As body size is related to larval nourishment, this suggests an effect of larval competition on the maintenance of polymorphism. 6. It is proposed that both the mating behaviour of this species (long copulations) and the existence of changes in population density during the season are the main factors that maintain the polymorphism in I. graellsii.

Do allopatric male Calopteryx virgo damselflies learn species recognition?

Kuitunen, K; Haukilehto, E; Raatikainen, KJ; Hakkarainen, H; Miettinen, M; Hogmander, H; Kotiaho, JS. 2012

There is a growing amount of empirical evidence that premating reproductive isolation of two closely related species can be reinforced by natural selection arising from avoidance of maladaptive **hybrid**ization. However, as an alternative for this popular reinforcement theory, it has been suggested that learning to prefer conspecifics or to discriminate heterospecifics could cause a similar pattern of reinforced premating isolation, but this possibility is much less studied. Here, we report results of a field experiment in which we examined (i) whether allopatric Calopteryx virgo damselfly males that have not encountered heterospecific females of the congener C. splendens initially show discrimination, and (ii) whether C. virgo males learn to discriminate heterospecifics or learn to associate with conspecifics during repeated experimental presentation of females. Our experiment revealed that there was a statistically nonsignificant tendency for C. virgo males to show initial discrimination against heterospecific females but because we did not use sexually naive individuals in our experiment, we were not able to separate the effect of innate or associative learning. More importantly, however, our study revealed that species discrimination might be further strengthened by learning, especially so that C. virgo males increase their association with conspecific females during repeated presentation trials. The role of learning to discriminate C. splendens females was less clear. We conclude that learning might play a role in species recognition also when individuals are not naive but have already encountered potential conspecific mates.

Divergence in female damselfly sensory structures is consistent with a species recognition function but shows no evidence of reproductive character displacement

Barnard, AA; Masly, JP. 2018

Males and females transmit and receive signals prior to mating that convey information such as sex, species identity, or individual condition. In some animals, tactile signals relayed during physical contact between males and females before and during mating appear to be important for mate choice or reproductive isolation. This is common among odonates, when a male grasps a female's thorax with his terminal appendages prior to copulation, and the female subsequently controls whether copulation occurs by bending her abdomen to complete intromission. It has been hypothesized that mechanosensory sensilla on the female thoracic plates mediate mating decisions, but is has been difficult to test this idea. Here, we use North American damselflies in the genus Enallagma (Odonata: Coenagrionidae) to test the hypothesis that variation in female sensilla traits is important for species recognition. Enallagma anna and E. carunculatum **hybrid**ize in nature, but experience strong reproductive isolation as a consequence of divergence in male terminal appendage morphology. We quantified several mechanosensory sensilla phenotypes on the female thorax among multiple populations of both species and compared divergence in these traits in sympatry versus allopatry. Although these species differed in features of sensilla distribution within the thoracic plates, we found no strong evidence of reproductive character displacement among the sensilla traits we measured in regions of sympatry. Our results suggest that species-specific placement of female mechanoreceptors may be sufficient for species recognition, although other female sensory phenotypes might have diverged in sympatry to reduce interspecific **hybrid**ization.

A General Explanation for the Persistence of Reproductive Interference

Drury, JP; Anderson, CN; Castillo, MBC; Fisher, J; McEachin, S; Grether, GF. 2019

Reproductive interference is widespread, despite the theoretical expectation that it should be eliminated by reproductive character displacement (RCD). A possible explanation is that females of sympatric species are too similar phenotypically for males to distinguish between them, resulting in a type of evolutionary dilemma or catch-22 in which reproductive interference persists because male mate recognition (MR) cannot evolve until female phenotypes diverge further, and vice versa. Here we illustrate and test this hypothesis with data on rubyspot damselflies (Hetaerina spp.). First, reproductive isolation owing to male MR breaks down with increasing interspecific similarity in female phenotypes. Second, comparing allopatric and sympatric populations yielded no evidence for RCD, suggesting that parallel divergence in female coloration and male MR in allopatry determines the level of reproductive isolation on secondary contact. Whenever reproductive isolation depends on male MR and females of sympatric species are phenotypically similar, the evolutionary catch-22 hypothesis offers an explanation for the persistence of reproductive interference.

Reinforcement: A new perspective on an old controversy

Hostert, EE. 1997

A critical component of the reinforcement model, incomplete postzygotic reproductive isolation, has been overlooked in the many selection experiments designed to test this model. Many field observations are consistent with the reinforcement model, but theoretical work predicts that reinforcement should only work when nearly

complete postzygotic reproductive isolation has developed. The experiments described here used four levels of postzygotic reproductive isolation: complete, strong, moderate, and none. A significant decrease in heterotypic matings occurred over 25 generations in the complete postzygotic reproductive isolation treatment. No evidence for reinforcement was found in any of the other treatments using incomplete postzygotic reproductive isolation.

Hybridization in Calopteryx damselflies: the role of males

Tynkkynen, K; Grapputo, A; Kotiaho, JS; Rantala, MJ; Vaananen, S; Suhonen, J. 2008

Females are often considered responsible for **hybrid**ization between two species because usually they are the choosier sex and their cooperation is needed for successful copulation. However, males can also be responsible for **hybrid**ization, for example in species in which males are able to force copulation. We studied the pattern of **hybrid**ization in two congeneric damselfy species, Calopteryx splendens and Calopteryx virgo, and provide evidence that F-1 **hybrid**s between the two damselfly species occur in the wild. According to mitochondrial DNA analysis, **hybrid**ization is reciprocal: five of seven **hybrid**s were sired by C. splendens and two by C. virgo males. We conducted an experiment that revealed that males of both species have surprisingly poor premating reproductive isolation in that they accept heterospecific females, but C. splendens males were less discriminating against con- and heterospecific females than were C. virgo males. Moreover, our data on the number of **hybrid**s sired by either species in the wild are congruent with the results of the discrimination experiment, supporting the conclusion that males may be responsible for the **hybrid**ization. Our results suggest that the males' role in **hybrid**ization studies should no longer be neglected. (C) 2007 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Hybridization rate and climate change: are endangered species at risk?

Sanchez-Guillen, RA; Munoz, J; Hafernik, J; Tierney, M; Rodriguez-Tapia, G; Cordoba-Aguilar, A. 2014

Many species are altering their geographic range due to climate change creating new sympatric populations of otherwise allopatric populations. We investigated whether climate change will affect the distribution and thus the pattern of **hybrid**ization between two pairs of closely related damselfly species [Ischnura damula and I. demorsa, and I. denticollis and I. gemina (this, an endangered species)]. Thus, we estimated the strength of pre and postmating reproductive barriers between both pairs of species, and we predicted future potential distribution under four different Global Circulation Models and a realistic emissions scenario of climate change by using maximum entropy modelling technique. Our results showed that reproductive isolation (RI) is complete in I. damula x I. demorsa individuals: F-1 (first generation) **hybrid**s are produced but do not reach sexual maturation. However, RI in I. denticollis x I. gemina **hybrid**s is high but incomplete and unidirectional: only I. gemina females produced F-1 **hybrid**s which mate with males and females of I. denticollis and between them producing BC1 (back-crosses) and F-2 (second generation) viable **hybrid**s. Maximum entropy models revealed a northern and westward shift and a general reduction of the potential geographic ranges. Based on the pattern of **hybrid**ization, for I. damula and I. demorsa there is a current threat as well as a rapid displacement and/or extinction of I. gemina by I. denticollis. However, the current pattern of extinction may not continue due to the contraction in ranges of the four species.

Climate-Induced Range Shifts and Possible Hybridisation Consequences in Insects

Sanchez-Guillen, RA; Munoz, J; Rodriguez-Tapia, G; Arroyo, TPF; Cordoba-Aguilar, A. 2013

Many ectotherms have altered their geographic ranges in response to rising global temperatures. Current range shifts will likely increase the sympatry and **hybrid**isation between recently diverged species. Here we predict future sympatric distributions and risk of **hybrid**isation in seven Mediterranean ischnurid damselfly species (I. elegans, I. fountaineae, I. genei, I. graellsii, I. pumilio, I. saharensis and I. senegalensis). We used a maximum entropy modelling technique to predict future potential distribution under four different Global Circulation Models and a realistic emissions scenario of climate change. We carried out a comprehensive data compilation of reproductive isolation (habitat, temporal, sexual, mechanical and gametic) between the seven studied species. Combining the potential distribution and data of reproductive isolation at different instances (habitat, temporal, sexual, mechanical and gametic), we infer the risk of **hybrid**isation in these insects. Our findings showed that all but I. graellsii will decrease in distributional extent and all species except I. senegalensis are predicted to have northern range shifts. Models of potential distribution predicted an increase of the likely overlapping ranges for 12 species combinations, out of a total of 42 combinations, 10 of which currently overlap. Moreover, the lack of complete reproductive isolation and the patterns of **hybrid**isation detected between closely related ischnurids, could lead to local extinctions of native species if the **hybrid**s or the introgressed colonising species become more successful.

Non-ecological speciation, niche conservatism and thermal adaptation: how are they connected?

Svensson, EI. 2012

During the last decade, the ecological theory of adaptive radiation, and its corollary "ecological speciation", has been a major research theme in evolutionary biology. Briefly, this theory states that speciation is mainly or largely the result of divergent selection, arising from niche differences between populations or incipient species. Reproductive isolation evolves either as a result of direct selection on mate preferences (e.g. reinforcement), or as a correlated response to divergent selection ("by-product speciation"). Although there are now many tentative examples of ecological speciation, I argue that ecology's role in speciation might have been overemphasised and that non-ecological and non-adaptive alternatives should be considered more seriously. Specifically, populations and species of many organisms often show strong evidence of niche conservatism, yet are often highly reproductively isolated from each other. This challenges niche-based ecological speciation and reveals partial decoupling between ecology and reproductive isolation. Furthermore, reproductive isolation might often evolve in allopatry before ecological differentiation between taxa or possibly through learning and antagonistic sexual interactions, either in allopatry or sympatry. Here I discuss recent theoretical and empirical work in this area, with some emphasis on odonates (dragonflies and damselflies) and suggest some future avenues of research. A main message from this paper is that the ecology of species differences is not the same as ecological speciation, just like the genetics of species differences does not equate to the genetics of speciation.

Survival rates in a natural population of the damselfly Ceriagrion tenellum: effects of sex and female phenotype

Andres, JA; Rivera, AC. 2001

1. Ceriagrion tenellum females show genetic colour polymorphism. Androchrome (erythrogastrum) females are brightly (male-like) coloured while gynochrome females (typica and melanogastrum) show cryptic colouration. 2. Several hypotheses have been proposed to explain the existence of more than one female morph in damselfly populations. The reproductive isolation and intraspecific mimicry hypotheses predict greater survival of gynochrome females, while the density dependent hypothesis predicts no differential survival between morphs. 3. Mature males had greater recapture probability than females while the survival probability was similar for both sexes. Survival and recapture rates were similar for androchrome and gynochrome females. 4. Gynochrome females showed greater mortality or migration rate than androchrome females during the pre-reproductive period. This result is not predicted by the above hypotheses or by the null hypothesis that colour polymorphism is only maintained by random factors: founder effects, genetic drift, and migration.

The tempo and mode of three-dimensional morphological evolution in male reproductive structures

McPeek, MA; Shen, L; Torrey, JZ; Farid, H. 2008

Various evolutionary forces may shape the evolution of traits that influence the mating decisions of males and females. Phenotypic traits that males and females use to judge the species identify of potential mates should evolve in a punctuated fashion, changing significantly at the time of speciation but changing little between speciation events. In contrast, traits experiencing sexual selection or sexually antagonistic interactions are generally expected to change continuously over time because of the directional selection pressures imposed on one sex by the actions of the other. To test these hypotheses, we used spherical harmonic representations of the shapes of male mating structures in reconstructions of the evolutionary tempo of these structures across the history of the Enallagma damselfly clade. Our analyses show that the evolution of these structures is completely consistent with a punctuated model of evolutionary change and a constant evolutionary rate throughout the clade's history. In addition, no interpopulation variation in shape was detected across the range of one species. These results indicate that male mating structures in this genus are used primarily for identifying the species of potential mates and experience little or no selection from intraspecific sexual selection or sexual antagonism. The implications of these results for speciation are discussed.

Inheritance, distribution and genetic differentiation of a color polymorphism in Panamanian populations of the tortoise beetle, Chelymorpha alternans (Coleoptera: Chrysomelidae)

Strickland, LR; Arias, CF; Rodriguez, V; Johnston, JS; McMillan, WO; Windsor, D. 2019

Intraspecific variation maintained in natural populations has long intrigued scientists and naturalists. One form of this variation, color polymorphisms, provide a rich opportunity to connect genotypic and phenotypic diversity within an ecological and evolutionary context. The existence of color polymorphisms in Panamanian populations of the Neotropical tortoise beetle, Chelymorpha alternans, has been suspected but never systematically explored. To characterize geographic distribution and underlying genetics we sampled a total of 3819 beetles from 28 sites across Panama, quantifying five distinct phenotypes. Two phenotypes, the "metallic" and "rufipennis" are the most widely distributed phenotypes, occurring in nearly all collecting sites. The "veraguensis" phenotype was found to be restricted to the Western end of the Isthmus and the "militaris" phenotypes restricted to sites east of the canal. Controlled matings between phenotypes and reared offspring revealed no indications of reproductive barriers, even among phenotypes which do not co-occur in nature. Color pattern phenotype is largely controlled by Mendelian assortment of four alleles competing at a single locus. A clear dominance hierarchy exists among alleles, with two being co-dominant. Genomic scans from 32 individuals revealed low levels of genetic differentiation, with a small fraction of the genome showing a high degree of divergence. The easily observed variation among populations, simple genetic architecture, and rearing capabilities, make this a promising system for investigating proximate and ultimate factors of phenotypic variation.

Isolation barriers and genetic divergence in non-territorial Argia damselflies

Nava-Bolanos, A; Sanchez-Guillen, RA; Munguia-Steyer, R; Cordoba-Aguilar, A. 2017

Isolation barriers work at different instances during the mating process in odonate insects. In territorial damselflies, heterospecific interactions are mainly precluded by sexual (visual) isolation, while in non-territorial damselflies, heterospecific interactions are mostly precluded by mechanical isolation and sexual (tactile) isolation. In this study we investigated the strength of three premating barriers (visual, mechanical and tactile), genetic divergence and degree of sympatry (on their entire distribution) between four non-territorial Argia damselflies (A. anceps, A. extranea, A. oenea and A. tezpi). Our results are explained in the light of learned mating preferences and Kaneshiro's hypothesis. We detected a strong reproductive isolation between all pairs of species by the joint action of the three studied barriers [visual (90.6%), mechanical (8.7%) and tactile (0.7%)]. Sexual (visual) isolation was the most important barrier, perhaps driven by learning mating preferences. One of the studied species, A. extranea, which is the most derived of the studied species, showed a highly asymmetric isolation in reciprocal crosses, which is consistent with Kaneshiro's hypothesis. Moreover, we detected a negligible ecological niche differentiation between the studied species (70% of shared distribution). Our results suggest that sexual (visual) selection may be an important force driving speciation in non-territorial species. (C) 2016 The Linnean Society of London.

Patterns of Phenotypic Divergence in Wing Covariance Structure of Calopterygid Damselflies

Eroukhmanoff, F; Outomuro, D; Ocharan, FJ; Svensson, EI. 2009

Comparing species differences in covariance patterns of traits subject to divergent selection pressures can increase our understanding to the mechanisms of phenotypic divergence. Different species of calopterygid damselflies have diverged in the melanized wing patch of males. This trait serves multiple ecological functions and has behavioral consequences in terms of sexual selection, interspecific interactions, reproductive isolation. We compared the phenotypic variance-covariance matrices (P) of wing traits among nine populations of four European species of calopterygid damselflies. We found modest divergence in covariance structure among populations of the same species, but strong divergence between species. Interestingly, the orientation of the first eigenvector of P (P (max)) differed more between closely related species than between distantly related species, although this pattern was absent when overall covariance structures were compared. We also found that distantly related species but geographically closer had converged towards a similar covariance structure. Finally, divergence in covariance structure was correlated with divergence in wing patch length, but not with other wing traits. This last finding suggests that divergent selection on wing patch length might have affected the stability of P. These results indicate that P might not only reflect ancestral developmental pathways but might also be influenced by current ecology.

Interspecific aggression, not interspecific mating, drives character displacement in the wing coloration of male rubyspot damselflies (Hetaerina)

Drury, JP; Grether, GF. 2014

Traits that mediate intraspecific social interactions may overlap in closely related sympatric species, resulting in costly between-species interactions. Such interactions have principally interested investigators studying the evolution of reproductive isolation via reproductive character displacement (RCD) or reinforcement, yet in addition to reproductive interference, interspecific trait overlap can lead to costly between-species aggression. Previous research on rubyspot damselflies (Hetaerina spp.) demonstrated that sympatric shifts in male wing colour patterns and competitor recognition reduce interspecific aggression, supporting the hypothesis that agonistic character displacement (ACD) drove trait shifts. However, a recent theoretical model shows that RCD overshadows ACD if the same male trait is used for both female mate recognition and male competitor recognition. To determine whether female mate recognition is based on male wing coloration in Hetaerina, we conducted a phenotype manipulation experiment. Compared to control males, male H. americana with wings manipulated to resemble a sympatric congener (H. titia) suffered no reduction in mating success. Thus, female mate recognition is not based on species differences in male wing coloration. Experimental males did, however, experience higher interspecific fighting rates and reduced survival compared to controls. These results greatly strengthen the case for ACD and highlight the mechanistic distinction between ACD and RCD.

Molecular population divergence and sexual selection on morphology in the banded demoiselle (Calopteryx splendens)

Svensson, EI; Kristoffersen, L; Oskarsson, K; Bensch, S. 2004

The importance of sexual selection in population divergence is of much interest, mainly because it is thought to cause reproductive isolation and hence could lead to speciation. Sexually selected traits have been hypothesized to diverge faster between populations than other traits, presumably because of differences in the strength, mechanism or dynamics of selection. We investigated this by quantifying population divergence in eight morphological characters in 12 south Swedish populations of a sexually dimorphic damselfly, the banded demoiselle (Calopteryx splendens). The morphological characters included a secondary sexual character, the male melanized wing spot, which has an important function in both inter- and intrasexual selection. In addition, we investigated molecular population divergence, revealed by amplified fragment length polymorphism (AFLP) analysis. Molecular population divergence was highly significant among these Northern European populations (overall F-st = 0.054; pairwise population F-st's ranged from similar to0 to 0.13). We found evidence for isolation-by-distance (r = 0.70) for the molecular markers and a significant correlation between molecular and phenotypic population divergence (r = 0.39). One interpretation is that population divergence for the AFLP loci are affected by genetic drift, but is also indirectly influenced by selection, due to linkage with loci for the phenotypic traits. Field estimates of sexual and natural selection from two of the populations revealed fairly strong sexual selection on wing spot length, indicating that this trait has the potential to rapidly diverge, provided that variation is heritable and the observed selection is chronic.

Adaptive loss of color polymorphism and character displacements in sympatric Mnais damselflies

Tsubaki, Y; Okuyama, H. 2016

A geographical survey of two Mnais damselfly species in the Kinki area of Japan showed evidence for character displacements when the two species were found in sympatry. Mnais costalis, a species that has polymorphic male mating types of orange-winged territorial and clear-winged non-territorial morphs (hereafter abbreviated to orange and clear morphs respectively) in allopatry often shifted to having monomorphic orange morphs in sympatry. The mean body size of orange morphs was consistently larger than that of clear morph in allopatry. The mean body size of the sympatric orange morphs was even larger than that of allopatric orange morphs. By contrast, Mnais pruinosa, a species that also has two morphs of large orange and small clear morphs in allopatry, shifted to having monomorphic clear morphs in sympatry. The mean body size of the sympatric clear morphs was smaller than that of allopatric clear morphs. Divergence was also detected in the preference for habitat insolation conditions between sympatric Mnais damselflies. Both species in allopatric regions prefer half-light forest habitats, while in sympatric regions they showed diversified habitat preference: M. costalis preferred sunny habitats while M. pruinosa preferred shady habitats. Multiple character displacements in signal traits and habitat preference emerged in heterogeneous forest light environments are likely to have synergistic effects on the reproductive isolation of the two species.
