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### AN UNUSUAL SONG-PATTERN IN THE CHORTHIPPUS-MOLLIS GROUP (ORTHOPTERA, ACRIDIDAE) - LOCAL VARIANT OR HYBRID POPULATION

RAGGE, DR. 1981

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### GENETIC DIFFERENTIATION, HYBRIDIZATION AND REPRODUCTIVE ISOLATION IN MYGALOPSIS-MARKI BAILEY (ORTHOPTERA, TETTIGONIIDAE)

DADOUR, IR; JOHNSON, MS. 1983

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### THE MEIOTIC BEHAVIOR OF NATURAL F1 HYBRIDS BETWEEN TRIMEROTROPIS-SUFFUSA SCUDDER AND TRIMEROTROPIS-CYANEIPENNIS BRUNER (ORTHOPTERA, OEDIPODINAE)

JOHN, B; LIGHTFOOT, DC; WEISSMAN, DB. 1983

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### THE LE BROC GRASSHOPPER POPULATION - FURTHER EVIDENCE OF ITS HYBRID STATUS (ORTHOPTERA, ACRIDIDAE)

RAGGE, DR. 1984

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### A HYBRID ZONE BETWEEN CHORTHIPPUS-PARALLELUS-PARALLELUS AND CHORTHIPPUS-PARALLELUS-ERYTHROPUS (ORTHOPTERA, ACRIDIDAE) - BEHAVIORAL CHARACTERS

BUTLIN, RK; HEWITT, GM. 1985

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### A HYBRID ZONE BETWEEN CHORTHIPPUS-PARALLELUS-PARALLELUS AND CHORTHIPPUS-PARALLELUS-ERYTHROPUS (ORTHOPTERA, ACRIDIDAE) - MORPHOLOGICAL AND ELECTROPHORETIC CHARACTERS

BUTLIN, RK; HEWITT, GM. 1985

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### ON THE REPRODUCTIVE, CHROMOSOMAL AND MORPHOMETRIC RELATIONSHIPS OF THE SO-CALLED DRY-SEASON AND WET-SEASON MENDELIAN POPULATIONS OF THE VARIEGATED GRASSHOPPER, ZONOCERUS-VARIEGATUS (ORTHOPTERA, PYROGOMORPHIDAE) AND THEIR HYBRID

IHEAGWAM, EU; ENEOBONG, EE. 1985

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### A HYBRID ZONE BETWEEN CHORTHIPPUS-PARALLELUS PARALLELUS AND CHORTHIPPUS-PARALLELUS ERYTHROPUS (ORTHOPTERA, ACRIDIDAE) - CHROMOSOMAL DIFFERENTIATION

GOSALVEZ, J; LOPEZFERNANDEZ, C; BELLA, LJ; BUTLIN, RK; HEWITT, GM. 1988

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### ASSORTATIVE MATING ACROSS A HYBRID ZONE IN CHORTHIPPUS-PARALLELUS (ORTHOPTERA, ACRIDIDAE)

RITCHIE, MG; BUTLIN, RK; HEWITT, GM. 1989

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### GENETIC COMPATIBILITY AND GEOGRAPHIC PROFILE OF 2 CLOSELY RELATED SPECIES OF ALLONEMOBIUS (GRYLLIDAE, ORTHOPTERA)

TANAKA, S. 1991

Genetic compatibility between two species of ground crickets, *Allonemobius fasciatus* De Geer and *A. socius* Scudder, was studied by crossing experiments. Reciprocal crosses produced viable offspring. However, the number of eggs produced by *A. fasciatus* (female) x *A. socius* (male) was significantly smaller than that by the reciprocal cross or intraspecific crosses; the hatchability was < 10 %, whereas most eggs produced in the other crosses overwintered and hatched. In the laboratory, development time for the male hybrids produced by *A. socius* (female) x *A. fasciatus* (male) was similar to that of their mothers rather than fathers, but the hybrid females were intermediate between the parent species, suggesting that nymphal development is primarily controlled by the X chromosome. The two species and their hybrids showed different ranges of embryonic stages for water absorption and diapause. Crickets collected from different localities in eastern North America were identified to species by their different diapause stages. The results were consistent with others' observations that the two species meet at around 38-39-degrees-N where hybrids occur. The geographic profiles and the possible isolating mechanisms between the two species are discussed.

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### COMPARISONS AMONG MORPHOLOGICAL CHARACTERS AND BETWEEN LOCALITIES IN THE CHORTHIPPUS-PARALLELUS HYBRID ZONE (ORTHOPTERA, ACRIDIDAE)

BUTLIN, RK; RITCHIE, MG; HEWITT, GM. 1991

Two subspecies of the grasshopper, *Chorthippus parallelus*, meet and hybridize in the Pyrenees. The hybrid zone between the two taxa is believed to have formed following range expansion at the end of the last glaciation and to be maintained by a balance between gene flow and selection against hybrids. Laboratory F1 hybrid males are sterile. We have examined morphological characters in two cols about 200 km apart and compared the positions and widths of clines for these characters both within and between cols. Clines are neither coincident (centred in the same position), nor concordant equal in width) in either col. Furthermore clines are wider and more dispersed in the western col. The lack of concordance can be explained on several models for the maintenance of the hybrid zone and is a common observation. There are many fewer examples of lack of coincidence and this result is more difficult to interpret. We suggest that it is due to a difference in population structure between the cols: a patchy distribution of grasshoppers in the western col produces wider, more dispersed clines while a sharp break in distribution in the eastern col tends to concentrate morphological change over a shorter distance.

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#### **CALLING SONG DISPLACEMENT IN A ZONE OF OVERLAP AND HYBRIDIZATION**

BENEDIX, JH; HOWARD, DJ. 1991

The ground crickets *Allonemobius fasciatus* and *A. socius* meet in a mosaic zone of overlap and hybridization stretching from the East Coast to at least Illinois. To test whether male calling song differences were enhanced in sympatry, we analyzed the songs of crickets from inside and outside the zone of overlap along two transects. No evidence of calling song displacement was found in *A. socius* males from populations within the zone of overlap. On the other hand, *A. fasciatus* displayed calling song displacement in three populations. Our results are consistent with the hypothesis that the selective pressure exerted by the challenge from a related species is frequency dependent. While not a conclusive demonstration, the observed shifts in calling song are strongly suggestive of reproductive character displacement.

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#### **HYBRIDIZATION STUDIES IN THE MIGRATORY GRASSHOPPER MELANOPLUS-SANGUINIPES (F) (ACRIDIDAE)**

CHAPCO, W. 1991

Three subspecies of the migratory grasshopper *Melanoplus sanguinipes* (F.) are recognized by Gurney and Brooks (1959) who, on the basis of morphology and presence of intergrades in collections, do not consider the taxa sufficiently different to warrant according them species status. Present experiments show that members of distant populations, when crossed, readily produce viable and fertile hybrids of both sexes. It is, however, premature to claim that the groups are conspecific without confirmatory information on, for instance, genetic distances and mating discrimination indices. Nonetheless, it is hypothesized that these parameters are expected to have low values given the hybridization results.

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#### **CYTOGENETICS OF 2 INTERSPECIFIC SYNTHETIC HYBRIDS OF THE GRASSHOPPER GENUS EUCHORTHIPPUS**

SANTOS, JL; ARANA, P; HENRIQUESGIL, N. 1991

The spermatogenesis of two synthetic hybrid individuals of the grasshopper genus *Euchorthippus* was studied by C-banding methods. One resulted from the cross *Euchorthippus pulvinatus* female x *Euchorthippus chopardi* male (p/c), whereas the other one was produced in the corss *E. chopardi* female x *E. pulvinatus* male (c/p). The two parental sets of chromosomes were always recognized according to their different C-banding patterns. Chiasma frequency was decreased in both hybrids when compared with the parental species, this decrease being more accentuated in the hybrid individual c/p, where univalents at metaphase I were frequent. Chiasmata were formed between homoeologous chromosomes, and only two multivalent associations were observed. Polyploid spermatids and some micronuclei were a common feature in both hybrids. It is suggested that C-heterochromatin differences do not play any important role in the speciation process: genic differences between parental genomes are probably more important.

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#### **THE EFFECT OF A PARTIAL BARRIER ON THE MOVEMENT OF A HYBRID ZONE**

KOHLMANN, B; SHAW, D. 1991

Computer simulations of clines (Brues, 1972; Endler, 1977) as well as theoretical arguments (Nagylaki, 1975), have shown that steps in gene frequencies will be pulled to partial barriers (areas of reduced gene flow) if they form within approximately a cline width of the partial barrier. The behavior of a hybrid zone between two chromosomal taxa ("Moreton" and "Torresian") of the acridine grasshopper *Caledia captiva* in southeast Queensland has been analyzed and found to conform qualitatively with a model of altered gene flow patterns. Clines in four enzyme systems were analyzed for 1983 and 1986 along a transect across the hybrid zone. The clines have shifted towards an area of regenerating forest, while homozygote frequencies have increased at this point. This forest barrier has broken the continuity of the spatial distribution of *C. captiva*, forming population islands in part of the hybrid zone, and thus reducing the amount of gene flow. The distance between the barrier and the original cline is approximately of the order of a cline width, so that they would be expected to interact. Historical information suggests that the secondary contact between the "Moreton" and "Torresian" taxa occurred very recently (1844-1940), due to the intensive land-clearing activities during the European settlement.

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#### **HYBRID BREAKDOWN IN PEROMYSCUS-LEUCOPUS AND EXAMINATION OF THE RECOMBINATIONAL-BREAKDOWN MODEL**

ADKINS, RM; MCBEE, K; PORTER, CA; BAKER, RJ. 1991

The recombinational-breakdown model is based on disruption of normal recombinational patterns and increased rates of mutation in hybrids between chromosomally distinct morphs of a species. A hybrid zone between northeastern and southwestern cytotypes of the white-footed mouse, *Peromyscus leucopus*, was used to examine how taxonomically widespread the implications of this model are. Aberration frequencies and the proportion of breaks in biarmed and acrocentric chromosomes were determined for mice from both pure-cytotypic populations, from a pure-hybrid locality, and from a site containing a mixture of pure-southwestern cytotypes and non-F1 hybrids. The pure-hybrid population had aberration frequencies significantly elevated above those of the southwestern population and the mixed parental-hybrid locality. Non-F1 hybrids within the pure-hybrid population had an elevated frequency of breaks in biarmed chromosomes. Breakdown, as measured by chromosomal aberrations, was maximal in the center of the hybrid zone. Such chromosomal disruption is a prediction of the recombinational-breakdown model. Therefore, the model appears to have applicability across broadly divergent taxonomic groups.

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#### **MULTIVALENTS RESULTING FROM MONOBRACHIAL HOMOLOGIES WITHIN A HYBRID ZONE IN DICHROPLUS-PRATENSIS (ACRIDIDAE) - MEIOTIC ORIENTATION AND SEGREGATION**

BIDAU, CJ. 1991

Natural populations of the South American grasshopper *Dichroplus pratensis* differ for seven polymorphic centric fusions involving the six longest telocentric

autosomes of the karyotype (L1-L6). Hence, the same telocentric is involved in more than one fusion in different populations producing metacentrics with monobrachial homologies. The present study concerns the meiotic behaviour of quadrivalents and quinquivalents formed in natural hybrids that occur in two hybrid zones between chromosomal races with monobrachial homologies. The analysis revealed that: (a) non-alternate orientation of multivalents at Metaphase I (MI) was high, ranging from 18.5 to 64.2% of the cells in 18 hybrid males. Non-alternate Prometaphase (PMI) orientation was studied in six males (two of each type of hybrid) and in all cases values were higher than in MI, which suggests reorientation between PMI and MI. (b) All hybrids showed high frequencies of aneuploid and diploid second spermatocytes which are the result of abnormal segregation and lagging of chromosomes involved in multivalent formation. A highly significant correlation exists between the frequency of abnormal MI cells per male and abnormal second division spermatocytes. In most individuals, however, the frequency of abnormal second spermatocytes was lower than that of abnormal MI, which suggests further reorientation of multivalents towards alternate orientation at MI or spermatocyte selection between both meiotic divisions. (c) The hybrids have an increased production of macrospermatids. The behaviour of the multivalents suggests that the inter-racial hybrids have their fertility moderately to severely reduced which infers the existence of post-mating reproductive isolation between races. This is discussed in relation to the maintenance and adaptive role of the fusion polymorphisms in nature.

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#### **BEHAVIORAL COUPLING IN TETTIGONIID HYBRIDS (ORTHOPTERA)**

RITCHIE, MG. 1992

Studies of the mating behavior of male and female F1 hybrids between closely related taxa can provide information concerning the genetic control of characters that play a major role in speciation. Orthoptera have been used previously for such studies. Hybrid crickets show behaviors which are broadly intermediate to the parentals but hybrid grasshoppers may retain parental behavior patterns. This study examines the behavior of hybrid *Ephippiger ephippiger* bushcrickets, the third major orthopteran group. The differences in male song and female preference are probably both mainly additive and male song differences not sex linked. Thus, given a choice, hybrid females would prefer to mate with hybrid males, an example of "behavioral coupling." The evolutionary inferences which can be drawn from studies of F1 hybrids between closely related taxa are discussed.

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#### **CALLING SONG AND SELECTIVE PHONOTAXIS IN THE FIELD CRICKETS, *GRYLLUS-FIRMUS* AND *G-PENNSYLVANICUS* (ORTHOPTERA, GRILLIDAE)**

DOHERTY, JA; STORZ, MM. 1992

The field cricket species, *Gryllus firmus* and *G. pennsylvanicus*, occur in a mosaic hybrid zone that roughly parallels the eastern slope of the Appalachian mountains in the northeastern United States. It is important to know what role, if any, the calling song plays in mate choice in sympatric and allopatric populations. In this report, we present results on the variability of calling song properties along transects across this hybrid zone. We also present the results of experiments on phonotactic selectivity of females from an allopatric population of *G. firmus*. The male calling song of allopatric *G. firmus* was significantly slower in temporal rhythm (i.e., chirp and pulse repetition rates) and lower in pitch (i. e., dominant frequency) than that of allopatric *G. pennsylvanicus*. Calling song properties of males recorded in the hybrid zone varied considerably in temporal and spectral properties. In two-stimulus (choice) phonotaxis experiments, allopatric females of *G. firmus* preferred synthetic calling songs with conspecific pulse repetition rates over songs that had lower and higher pulse rates. This preference persisted even when the sound pressure levels of alternative stimuli were unequal. Therefore, allopatric females of *G. firmus* can discriminate between conspecific and heterospecific calling songs. Whether or not this same selectivity is present in sympatric populations remains unclear. Investigations of phonotactic selectivity in other allopatric and sympatric populations of both species are currently under way.

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#### **EVOLUTIONARY DIVERGENCE IN DOLICHOPODA CAVE CRICKETS - A COMPARISON OF SINGLE COPY DNA HYBRIDIZATION DATA WITH ALLOZYMES AND MORPHOMETRIC DISTANCES**

ALLEGRUCCI, G; CACCONE, A; CESARONI, D; SBORDONI, V. 1992

In this paper we attempt to investigate relationships between the amount of genetic divergence in nuclear genes and the degree of morphological differentiation for different sets of characters in Dolichopoda cave crickets. Six populations representing five Dolichopoda species from Central and Southern Italy have been studied. The overall genetic divergence at nuclear genes was estimated both by single copy DNA-DNA hybridization and allozyme frequencies at 26 loci. Euclidean distances for two multivariate sets of morphometric variables: one describing body and appendage morphology, the other male epiphallus shape. Results showed a close agreement between the branching patterns of DELTA-Tm values from DNA hybridization and Nei's allozyme distance values. On the other hand, patterns of morphological divergence revealed independent trends, although the branching pattern based on epiphallus morphology matched to some extent the phylogenies inferred from molecular data. The relative value of molecular and morphological characters as reliable phylogenetic tracers was evaluated in relation to their dependence on evolutionary factors. Implications of these findings on the calibration of molecular clocks are also discussed. The absolute rate of molecular change based on scDNA was estimated to be at least 0.98% divergence/my/lineage. This result is in agreement with calibrations attempted on other insects. Estimates of time of divergence based on allozymes (Nei's D) were highly consistent with the estimate from geological data.

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#### **BROAD-SCALE MAPPING OF A HYBRID ZONE BETWEEN SUBSPECIES OF *CHORTHIPPUS-PARALLELUS* (ORTHOPTERA, ACRIDIDAE)**

BUTLIN, RK; FERRIS, C; GOSALVEZ, J; HEWITT, GM; RITCHIE, MG. 1992

#### **FITNESS CONSEQUENCES OF POTENTIAL ASSORTATIVE MATING INSIDE AND OUTSIDE A HYBRID ZONE IN *CHORTHIPPUS-PARALLELUS* (ORTHOPTERA, ACRIDIDAE) - IMPLICATIONS FOR REINFORCEMENT AND SEXUAL SELECTION THEORY**

RITCHIE, MG; BUTLIN, RK; HEWITT, GM. 1992

#### **NATURAL HYBRIDIZATION AS AN EVOLUTIONARY PROCESS**

ARNOLD, ML. 1992

#### **EFFECTS OF DELETIONS ON MITOTIC STABILITY OF THE PATERNAL-SEX-RATIO (PSR) CHROMOSOME FROM *NASONIA***

BEUKEBOOM, LW; REED, KM; WERREN, JH. 1992

Paternal-Sex-Ratio (PSR) is a B chromosome that causes all-male offspring in the parasitoid wasp *Nasonia vitripennis*. It is only transmitted via sperm of carrier males

and destroys the other paternal chromosomes during the first mitotic division of the fertilized egg. Because of haplodiploidy, the effect of PSR is to convert diploid (female) eggs into haploid eggs that develop into PSR-bearing males. The PSR chromosome was previously found to contain several families of repetitive DNA, which appear to be present in local blocks. PSR chromosomes with irradiation-induced deletions have decreased rates of transmission and increased variation in transmission. This study investigates whether these differences in transmission of deletion chromosomes are due to mitotic instability. Two deletion chromosomes (E306 and F316) and the wild-type PSR chromosome were examined. A cytogenetic assay of testes revealed that wild-type PSR males contained the chromosome in 98%-100% of their spermatocytes. Similar counts from carriers of two deletion chromosomes were lower and varied between individuals from 50%-100%. One F316 male did not contain the chromosome in any of its spermatocytes although the chromosome was present in somatic tissues based on hybridization to PSR-specific repetitive DNA. A molecular analysis of males found the wild-type PSR chromosome to be present in all somatic tissues. Tissue specific differences in the presence or PSR were found in several males from the two deletion lines. The results show that deletions can result in mosaicism due to increased mitotic instability of PSR. Such individuals sometimes partially or completely fail to transmit the chromosome. Patterns of mosaicism of 13 chromosomes in other organisms are discussed.

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#### Population cytogenetics

Hewitt, GM. 1992

Chromosome variants are well established as useful genetic markers and integral components both of the genetic structure of populations, and in speciation. The current explosion of molecular techniques is facilitating the localization of many DNA sequences, while a reassessment of the fitness of chromosome mutants challenges some classical views on polymorphism and polytypy. Recent experiments on hybrid zones and mathematical modelling have greatly clarified the formation and evolution of chromosome races.

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#### LABORATORY HYBRIDIZATION STUDIES OF ALLONEMOBIUS-FASCIATUS AND A-SOCIUS (ORTHOPTERA, GRYLLIDAE)

GREGORY, PG; HOWARD, DJ. 1993

Allonemobius fasciatus (De Geer) and A. socius (Scudder) are small ground-dwelling crickets that meet and hybridize, to a limited extent, in a mosaic contact zone stretching from New Jersey to at least as far west as Illinois. To determine whether there is selection against hybridization, we compared heterospecific and hybrid crosses with conspecific crosses with regard to offspring production, viability, and development. Parental, F1, and F2 heterospecific and hybrid crosses produced considerable numbers of offspring, although some cross classes produced significantly fewer offspring than conspecific crosses. Differences in the number of offspring produced between heterospecific or hybrid crosses and conspecific crosses could be attributed to differences in the number of eggs laid rather than to differences in the percentage hatching. The time of hatching, the time required to reach adulthood, and hatching-to-adult survival were similar in the various cross classes. Postzygotic barriers to gene exchange do not appear to be strong enough to account for the low number of hybrids found in mixed populations.

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#### DIVERGENCE IN MATE FINDING BEHAVIOR BETWEEN 2 SUBSPECIES OF THE MEADOW GRASSHOPPER CHORTHIPPUS-PARALLELUS (ORTHOPTERA, ACRIDIDAE)

NEEMS, RM; BUTLIN, RK. 1993

Two parapatric subspecies of the grasshopper Chorthippus parallelus form a hybrid zone in the Pyrenees. Partial assortative mating between subspecies must result from differences in elements of the sequence of behaviors that leads to mating. It was already known that the subspecies differ in the structure of the acoustic mating signal produced by males and in the amount of song produced under laboratory conditions. Here we investigate whether any differences exist in male mating strategies in the field, concentrating on the prediction that male C. p. erythropus sing less and compensate for this by active searching (males divide their time between singing and moving in search of females). Results of field observations show that the two subspecies do in fact allocate their time differently. C. p. erythropus males spend almost twice as much time moving around the habitat as C. p. parallelus males. Furthermore, C. p. parallelus males divide their time into long bouts of continuous singing alternating with periods of movement. C. p. erythropus males, on the other hand, sing in short bursts interspersed with movement. The possible reasons for this divergence in male mating behavior and its consequences are discussed.

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#### DIFFERENCES IN LEAF FEEDING ON CORN HYBRIDS BY THE DIFFERENTIAL GRASSHOPPER, MELANOPLUS-DIFFERENTIALIS (THOMAS)

HARVEY, TL; THOMPSON, CA. 1993

#### ONE-WAY INTROGRESSION OF A SUBSPECIFIC SEX-CHROMOSOME MARKER IN A HYBRID ZONE

FERRIS, C; RUBIO, JM; SERRANO, L; GOSALVEZ, J; HEWITT, GM. 1993

A hybrid zone occurs along the ridge of the Pyrenees between two subspecies of the meadow grasshopper Chorthippus parallelus. C-banding reveals differences between the chromosomes of these two subspecies, especially for the X chromosome. One C-band is closely associated with an active nucleolar organizing region (NOR) on the X chromosome of Cp. parallelus but is absent from Cp. erythropus and can be used as a marker to follow the NOR. The cline for this marker is very narrow (1 km) and shows remarkable non-coincidence with other clines. It is displaced to the south by 5 km at Col du Pourtalet and 15 km at Col de la Quillane. Recombinants between the marker and other subspecific bands occur but are infrequent. The causes and consequences of such non-coincidence of clines are discussed.

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#### A HYBRID ZONE BETWEEN 2 SUBSPECIES OF THE GRASSHOPPER CHORTHIPPUS-PARALLELUS ALONG THE PYRENEES - THE WEST END

BUNO, I; TORROJA, E; LOPEZFERNANDEZ, C; BUTLIN, RK; HEWITT, GM; GOSALVEZ, J. 1994

The grasshopper Chorthippus parallelus (Cp) has two distinct subspecies which meet along the Pyrenees forming a hybrid zone. As Cp is rarely found above 2000 m, the contact between the two subspecies must occur through valleys crossing the Pyrenees perpendicularly or at both ends of the mountain ridge. The contact zones in two valleys have already been studied in detail, Col de Portalet (Central Pyrenees) and Col de la Quillane (Eastern Pyrenees), and this paper analyses the structure of the contact zone at the western end of the Pyrenees. The study has been carried out using different chromosome markers obtained by C-banding and silver staining, both related to the sex chromosome. Although the structure of this contact zone, analysed using these two markers, is similar to that of the contact zones occurring in other valleys, it is much wider and some remarkable peculiarities in the shapes of the dunes have been detected. Additionally, hybrid-related sex chromosome markers detected in Portalet have not been found in the present sample.

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## **INTERSPECIFIC MICRODIVERGENCY IN MALE GENITALIA BETWEEN 2 SIBLING SPECIES OF THE BUSH-CRICKET GENUS HEXACENTRUS (ORTHOPTERA, TETTIGONIIDAE)**

INAGAKI, H; SUGIMOTO, T. 1994

In 2 partially sympatric bushcricket species, *Hexacentrus japonicus* Karny 1907 and *H. unicolor* 1831, the male genitalia in their shape as a whole are both nearly alike. The cerci, however, are stronger twisted in *H. japonicus* than in *H. unicolor*. This has been proved by SEM studies for populations of the sympatric part (Simizu) as well for those of allopatric parts of their distribution areas (Tama in *H. japonicus* and Kamisima in *H. unicolor*): Such a interspecific microdivergency does not hinder their casual hybridization (F1, F2) as has turned out with laboratory rearings. This betokens a very close kinship of these species, in the field reproductively isolated one from the other by specific calling songs.

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## **INHERITANCE OF BODY AND TESTIS SIZE IN THE BUSH-CRICKET POECILIMON-VELUCHIANUS RAMME (ORTHOPTERA, TETTIGONIIDAE) EXAMINED BY MEANS OF SUBSPECIES HYBRIDS**

REINHOLD, K. 1994

## **CLINES FOR HYBRID DYSFUNCTION IN A GRASSHOPPER HYBRID ZONE**

VIRDEE, SR; HEWITT, GM. 1994

Two subspecies of the grasshopper *Chorthippus parallelus* meet in the Pyrenees forming a hybrid zone several kilometers wide. Crosses between the two pure taxa result in sterile male offspring and normal females (i.e., Haldane's rule applies). However, no such dysfunction has been detected in hybrid males collected through the center of the hybrid zone. By assessing the level of dysfunction in the offspring of reciprocal crosses, it was possible to map lines for the genes responsible for dysfunction through the zone. This analysis shows that there is no abrupt transition between incompatible genomes in the field. Crosses were also made between females collected from a transect spanning the hybrid zone and pure males of both subspecies. This reveals noncoincident lines for dysfunction near the center of the hybrid zone such that the dysfunction expressed in the offspring of these crosses is less than expected from simple models. More complex models involving interaction among genes must be invoked. Also, the possibility exists that since the postglacial contact of these two grasshopper taxa, hybrid dysfunction has become ameliorated by the evolution of modifiers. This hybrid zone is thought to be a tension zone, maintained by a balance between selection against hybrid genotypes and dispersal into the zone center. The lessening of hybrid disadvantage over time through the breakdown of epistatic interactions by recombination or through modification could account for the general lack of dysfunction in held collected hybrids today.

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## **NUCLEAR-DNA INTROGRESSION ACROSS A PYRENEAN HYBRID ZONE BETWEEN PARAPATRIC SUBSPECIES OF THE GRASSHOPPER CHORTHIPPUS-PARALLELUS**

VAZQUEZ, P; COOPER, SJB; GOSALVEZ, J; HEWITT, GM. 1994

Two parapatric subspecies of the European grasshopper *Chorthippus parallelus* meet along the Pyrenees and form a hybrid zone. A nuclear DNA sequence marker (cpnl-1), involving the presence or absence of a 5 bp insertion, was found to differentiate between the two subspecies along either side of the High Pyrenees but further electrophoretic and sequence analyses revealed that considerable mixing of the subspecific genomes had occurred towards the western and eastern ends of the Pyrenees. The line for this marker was relatively narrow in two adjoining western central high cols (Peyrelue: 9.7 km and Portalet: 13.3 km) but was significantly wider in another central high col towards the east (Quillane: 42.3 km), indicating that a different combination of forces has been operating on this locus in different regions of the Pyrenees.

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## **VARIATION IN CUTICULAR HYDROCARBONS ACROSS A HYBRID ZONE IN THE GRASSHOPPER CHORTHIPPUS-PARALLELUS**

NEEMS, RM; BUTLIN, RK. 1994

Two subspecies of the meadow grasshopper *Chorthippus parallelus* form a hybrid zone across the mountains of the Pyrenees. The subspecies differ, amongst several other traits, in the composition of their cuticular hydrocarbons. These compounds are thought to be involved in chemical communication during courtship. Here we report that cuticular hydrocarbon composition differs between the sexes and that a narrow line for cuticular hydrocarbons separates the subspecies. The line centre is displaced 15 km north of the majority of lines reported for other characters. This unusual lack of coincidence is discussed with reference to its possible causes and its consequences for the sexual communication system of *Chorthippus parallelus*.

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## **THE GENETIC CONSEQUENCES OF LONG-DISTANCE DISPERSAL DURING COLONIZATION**

NICHOLS, RA; HEWITT, GM. 1994

Rare long distance dispersal may have little impact on gene frequencies in established populations but it can dramatically increase gene flow during episodes of range expansion. We model the invasion of new territory by genetically distinct populations of the same species to investigate the dynamics of such episodes. If long distance dispersal is sufficiently frequent, the populations do not spread as a wave of advance but instead found intermingled isolates. We argue that this process can explain many otherwise puzzling patterns in the geographical distribution of alleles.

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## **Hybridisation of tree weta on Banks Peninsula, New Zealand, and colour polymorphism within *Hemideina ricta* (Orthoptera: Stenopelmidae)**

MorganRichards, M; Townsend, JA. 1995

The two species of tree weta on Banks Peninsula, New Zealand, *Hemideina ricta* and *H. femorata*, are genetically distinct though morphologically similar. Our allozyme data coincide with species identification based on numbers of stridulatory ridges. However, *H. ricta* appears to be polymorphic for the presence of black markings on hind femora and abdominal tergites. At one location on Banks Peninsula, weta were collected that were heterozygous at all 11 loci that differ between *H. ricta* and those of *H. femorata*. The numbers of stridulatory ridges on these two individuals fall between those characterising *H. ricta* and *H. femorata*. We conclude that these two weta are first generation hybrids, and that the detection of only F1 hybrids suggests that they are probably sterile. Sex-linkage of phosphoglucosyltransferase is found to be conserved in this family.

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## **DIVERGENCE IN CUTICULAR HYDROCARBONS BETWEEN PARAPATRIC SUBSPECIES OF THE MEADOW GRASSHOPPER, CHORTHIPPUS-PARALLELUS**

## (ORTHOPTERA, ACRIDIDAE)

NEEMS, RM; BUTLIN, RK. 1995

Two subspecies of the grasshopper *Chorthippus parallelus* (Orthoptera; Acrididae) meet and form a hybrid zone in the Pyrenees. Here we investigate whether the subspecies differ in the blend of cuticular hydrocarbons. Such differences may function as chemical signals, being detected via contact chemoreception and used during mate choice as in other insects. Gas chromatography shows that the subspecies have diverged in the composition of their cuticular hydrocarbons. This difference between subspecies exists over and above variation in cuticular hydrocarbons among individual populations. The majority of the difference can be attributed to the relative amounts of a small group of compounds present in the cuticle. The possible consequences of this chemical divergence for mating encounters between the subspecies are discussed.

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## AN UNUSUAL MITOCHONDRIAL-DNA POLYMORPHISM IN THE CHORTHIPPUS-BIGUTTULUS SPECIES GROUP (ORTHOPTERA, ACRIDIDAE)

MASON, DJ; BUTLIN, RK; GACESA, P. 1995

Mitochondrial DNA restriction fragment patterns have been used to investigate the *Chorthippus biguttulus* group: a group of morphologically similar grasshopper species with very distinct male calling songs. Ten haplotypes were identified in 21 populations, representing six species. Haplotype diversity was as great within species, and in same case within populations, as it was among species and no clear geographical patterns of haplotype distribution were revealed. In the light of grasshopper range changes since the last glaciation it is unlikely that these data can be explained entirely by the retention of ancestral polymorphism. This suggests that hybridization has occurred during periods of grasshopper range expansion since the last glacial maximum, allowing mtDNA transfer between populations that have previously diverged in allopatry.

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## MOSAICISM FOR SISTER-CHROMATID HETEROGENEITY IN SEX-CHROMOSOMES FROM HYBRIDS OF 2 SUBSPECIES OF CHORTHIPPUS-PARALLELUS (ORTHOPTERA, ACRIDIDAE)

BUNO, I; LOPEZFERNANDEZ, C; MASON, PL; GOSALVEZ, J. 1995

## EVOLUTION OF THE CHORTHIPPUS-BIGUTTULUS GROUP (ORTHOPTERA, ACRIDIDAE) IN THE ALPS, BASED ON MORPHOLOGY AND STRIDULATION

INGRISCH, S. 1995

Males of *Chorthippus biguttulus* (LINNE, 1758), *C. brunneus* (THUNBERG, 1815), *C. mollis* (CHARPENTIER, 1825), *C. mollis ignifer* (RAMME, 1923), *C. eisenrauti* (RAMME, 1931) and an aberrant form of *C. brunneus* (Ticino-brunneus) are compared on the base of morphological and acoustical characters. Discriminating morphological characters are the width of the costal and subcostal fields, the index "costal: subcostal field", the index "combined width of costal and subcostal fields: tegmen length", the index "tegmen length: length of apical area", the index "tegmen length: postfemur length", and the number of stridulatory pegs. But even in a two-character analysis there is a gradual dine of characters from *C. brunneus* via Ticino-brunneus and *C. eisenrauti* to *C. biguttulus*. Moreover, the range of morphological characters of *C. m. ignifer* greatly overlaps with those of *C. eisenrauti*, Ticino-brunneus and *C. m. mollis*. With regard to spontaneous stridulation of the males, *C. eisenrauti* differs from *C. biguttulus* in having shorter verses which are more numerous per song and in a more irregular number of syllables per echeme, of which there are usually three in *C. biguttulus*. Ticino-brunneus differs from nominate *C. brunneus* in producing longer verses with a higher number of pulses. The range of the verse length of Ticino-brunneus also overlaps with that of *C. eisenrauti*. Stridulation of *C. m. mollis* has a soft ending as in the last echemes the tick-sound is absent; in *C. m. ignifer* the song ends abruptly with a tick in the last echeme, and some echemes with a different syllable pattern can be loosely added. *C. m. ignifer* is reestablished as a good subspecies on the basis of song characters. *C. eisenrauti* is regarded to be a sister species of *C. biguttulus* conserving many of the primitive characters of the *C. biguttulus* group. A zone of transient characters between *C. eisenrauti* and *C. biguttulus* exists between Bivio and Calanda (Grisons); and a transient zone between *C. eisenrauti* and *C. brunneus* between Bregaglia and the Upper Engadine. Ticino-brunneus possibly evolved by hybridisation between *C. eisenrauti* and *C. brunneus*. A hypothetical scheme of the evolution of the taxa of the *C. bigrcttulus* group occurring in the Alps is presented and discussed.

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## GENE EXCHANGE IN A GROUND CRICKET HYBRID ZONE

CHU, J; POWERS, E; HOWARD, DJ. 1995

The ground crickets *Allonemobius fasciatus* and *A. socius* (Orthoptera: Gryllidae) are sister species that form a mosaic hybrid zone in the eastern United States. The genetic structure of the hybrid zone has been studied extensively by the use of protein electrophoresis. Here, we report the discovery of several random amplification of polymorphic DNA (RAPD) markers that distinguish the two species, and we assess the congruence of RAPD markers and protein markers with regard to the identification of hybrids in mixed populations. Both sets of markers indicate that gene flow between *A. fasciatus* and *A. socius* is quite limited.

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## HYBRIDIZATION STUDIES ON BLATTELLA-GERMANICA AND B-ASAHINAI (DICTYOPTERA, BLATTELLIDAE) - CHIASMA FREQUENCY AND DISTRIBUTION

ROSS, MH; LIU, H. 1995

Chiasma frequency and distribution were studied in *Blattella asahinai* Mizukubo and interspecific hybrid males from crosses of *B. asahinai* X *B. germanica* (L.). Observations were made on male meiocytes in late diakinesis. Chiasmata were localized at or near the ends of the chromosomes in both species. Chiasma frequency was lower and less variable in *B. asahinai* than in *B. germanica*. In the interspecific hybrids, the frequency was closer to that of *B. asahinai* than *B. germanica*. Chiasmata in hybrids were redistributed into regions where chiasmata are rare in the parent species. Chiasma frequency and the range of variation in chiasma frequency and in the frequency of internal chiasmata were affected by the species of the maternal parent. The maternal influence may be the result of a nonreciprocal translocation that involves the X chromosome and that separates the two species.

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## Estimation of genetic flow in insects: The analysis of *Caledia captiva* (Orthoptera: Acrididae)

Kohlmann, B. 1996

An indirect method was used for analyzing patterns and levels of gene flow between two races of the Australian grasshopper *Caledia captiva* (Orthoptera: Acrididae). A site was chosen where two chromosomal races (Moreton and Torresian) of *C. captiva* meet and form an hybrid zone. Five of their enzyme systems were analyzed and the allozymic disequilibria at the centre of the hybrid zone were calculated for estimating the dispersal rates. The estimates produce a dispersal rate in the order of 93 (67-138) m (generation)<sup>-1/2</sup>. This result evidences a rather restricted gene flow level, concordant with the narrow hybrid zone formed between the two races.



Steep genetic dines that coincide with narrow hybrid zones are generally considered to have arisen either from a balance of selection gradients and gene flow, or from competitive effects. The existence of low genetic introgression levels in this species would appear to support the first possibility.

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#### **Identification of a hybrid zone between distinctive colour variants of the alpine weta *Hemideina maori* (Orthoptera: Stenopelmidae) on the rock and pillar range, southern New Zealand**

King, TM; Wallis, GP; Hamilton, SA; Fraser, JR. 1996

The weta *Hemideina maori* occurs as yellow (to the north), black (to the south) and intermediate colour variants on the Rock and Pillar range in New Zealand. Isozyme electrophoresis revealed little genetic variation, whereas RFLP analysis of an amplified mtDNA sequence uncovered two haplotypes correlating completely with colour in allopatry and nearly so in sympatry. Intermediates had one or other haplotype. The observed distribution of colour variation and mtDNA genotypes is characteristic of a hybrid zone, perhaps formed by secondary contact. Work is continuing to locate nuclear DNA markers and to study the genetic interactions of the colour variants.

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#### **Water absorption by diapause and nondiapause eggs in two *Velarifictorus* species (Orthoptera: Gryllidae)**

Niikawa, K; Takeda, M. 1996

The absorption of water occurs one third of the way through embryonic development both in the cricket, *Velarifictorus micado* (SAUSSURE) which has egg diapause and its sibling species, *V. sp.* which has nymphal diapause. Less water was absorbed by diapause eggs of *V. micado* than by nondiapause eggs of *V. sp.* Anoxia by CO<sub>2</sub> at different embryonic stages showed stage-specific requirements of oxygen for water absorption; the earlier the anoxia was imposed, the later the water absorption occurred. The absorption of water is probably controlled by genotype but not by the chorionic structure or cytoplasmic maternal factor, since frozen and thawed eggs of *V. sp.* lost weight more rapidly than those of *V. micado* and those of their hybrid lost water at an intermediate rate between the two.

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#### **Multiple mating in natural populations of ground crickets**

Gregory, PG; Howard, DJ. 1996

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#### **A hybrid zone between two subspecies of *Chorthippus parallelus*. X-chromosome variation through a contact zone**

Serrano, L; delaVega, CG; Bella, JL; LopezFernandez, C; Hewitt, GM; Gosálvez, J. 1996

Two grasshopper subspecies, *Chorthippus parallelus parallelus* (Cp) and *Chorthippus parallelus erythropus* (Cpe), meet along the Pyrenees where they hybridize and produce a hybrid zone. A contact zone located in the Col de Portalet has been analyzed for the distribution of chromosome markers on the sex (X) chromosome in pure and hybrid populations. C-banding allowed us to distinguish both pure subspecific forms and recombinant forms, and to demonstrate their different frequencies through the contact zone. Interestingly, the distal C-band (P) on the X chromosome that characterizes Cp individuals occurs at very high frequency through the zone and then drops sharply, close to where pure Cpe populations are found. A novel interstitial C-band (H) has been found, probably derived from that characterizing Cpe individuals (E). This marker band is only present in hybrid populations. These data are discussed in the light of the dynamics of the hybrid zone.

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#### **Life-history adaptation and reproductive isolation in a grasshopper hybrid zone**

Orr, MR. 1996

Patterns of life-history adaptation and reproductive isolation were investigated in the acridid grasshoppers *Melanoplus sanguinipes* and *M. devastator*, which hybridize along an altitudinal gradient in the Sierra Nevada of California. *Melanoplus sanguinipes* females crossed with *M. devastator* males produced eggs that were approximately half as viable as eggs from other crosses. Diminished viability was not attributable either to infection by *Wolbachia pipiensis* or to failure of sperm transfer. When offered an opportunity to choose a mate, females from all populations discriminated against males of the other species, whereas in no-choice tests measuring copulation duration only females from the tails of the dunes showed preferences. *Melanoplus sanguinipes*, found at high elevations where the growing season is short, exhibited faster egg hatch, faster larval development, smaller adult body sizes, and smaller clutch sizes than *M. devastator*. *Melanoplus devastator*, from California's Central Valley, endured a hot and dry summer in a reproductive diapause that was absent in *M. sanguinipes*. Clines in reproductive diapause and clutch size coincided with the region of reproductive incompatibility. Development time, body size, and hatch time also changed across the hybrid zone, but the regions of largest transitions in these traits were either difficult to locate using the limited populations studied here or were not coincident with the zone's center. A method is described for combining ecological and phylogenetic analyses to address the unknown issue of whether life-history divergence has contributed to reproductive isolation in this system.

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#### **Strictly parapatric distribution of flightless leaf beetles of the *Chrysolina angusticollis* species complex (Coleoptera, Chrysomelidae) in the vicinity of Sapporo, northern Japan**

Saitoh, S; Katakura, A. 1996

In the southwestern suburbs of Sapporo, northern Japan, the flightless leaf beetle *Chrysolina angusticollis* species complex is represented by three phenotypically distinct forms which are distributed in a strictly parapatric manner. Boundaries between the forms usually coincided with narrow topographic barriers such as streams and cliffs, and areas with low density of host plants. In only four out of 237 sites was more than one form discovered in sympatry. In these exceptional sites, putative hybrid individuals were also found. This strictly parapatric distribution and coincidence of boundaries with topographic barriers suggest that the boundaries are tension zones, i.e. hybrid zones maintained by dispersal of native individuals from outside of the zones and selection against hybrids in the zones. (C) 1996 The Linnean Society of London

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#### **Some genetic consequences of ice ages, and their role in divergence and speciation**

Hewitt, GM. 1996

The genetic effects of pleistocene ice ages are approached by deduction from paleoenvironmental information, by induction from the genetic structure of populations and species, and by their combination to infer likely consequences. (1) Recent palaeoclimatic information indicate rapid global reversals and changes in ranges of

species which would involve elimination with spreading from the edge. Leading edge colonization during a rapid expansion would be leptokurtic and lead to homozygosity and spatial assortment of genomes. In Europe and North America, ice age contractions were into southern refugia, which would promote genome reorganization. (2) The present day genetic structure of species shows frequent geographic subdivision, with parapatric genomes, hybrid zones and suture zones. A survey of recent DNA phylogeographic information supports and extends earlier work. (3) The grasshopper *Chorthippus parallelus* is used to illustrate such data and processes. Its range in Europe is divided on DNA sequences into five parapatric races, with southern genomes showing greater haplotype diversity - probably due to southern mountain blocks acting as refugia and northern expansion reducing diversity. (4) Comparison with other recent studies shows a concordance of such phylogeographic data over pleistocene time scales. (5) The role that ice age range changes may have played in changing adaptations is explored, including the limits of range, rapid change in new invasions and refugial differentiation in a variety of organisms. (6) The effects of these events in causing divergence and speciation are explored using *Chorthippus* as a paradigm. Repeated contraction and expansion would accumulate genome differences and adaptations, protected from mixing by hybrid zones, and such a composite mode of speciation could apply to many organisms. (C) 1996 The Linnean Society of London

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#### **On the origin of B-chromosomes: neo XY systems and X-like supernumeraries in Orthoptera**

Colombo, PC; Remis, MI. 1997

In previous diversification mechanisms of B-chromosomes were advanced, and conditions for their origin were summarized (GREEN 1990). In the present work, some examples of B-chromosomes in *statu nascendi* in grasshoppers with neo XY systems are cited, including two cases described in the present work (*Sinipta dalmani* and *Leptysma* sp.). It was earlier proposed that increased tolerance to supernumerary Xs due to dosage compensation could contribute to the common occurrence of X-like B-chromosomes within the Orthoptera. This seems to be more frequent among newly arisen neo XY systems, possibly due to X-nondisjunction in heterozygous or hybrid females. Mechanisms of differentiation of X-like Bs are further exemplified in *Leptysema argentina* and *Cylindrotettix obscurus*. It is also pointed out that small Bs could originate from polysomy of the smallest chromosomes, tolerated because of the few genes involved (exemplified in *Cylindrotettix obscurus*). Finally, the minute-B category is attributed to residual fragments from whole arm rearrangements, as in *Sinipta dalmani*, a species with a high frequency of spontaneous and polymorphic rearrangements.

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#### **Changes of insecticide resistance levels and detoxication enzymes following insecticide selection in the German cockroach, *Blattella germanica* (L.)**

Scharf, ME; Neal, JJ; Bennett, GW. 1997

Insecticide resistance in the German cockroach can be mediated by a number of mechanisms, the most common bring enhanced enzymatic metabolism. Changes in metabolic enzymes following insecticide selection of a hybrid German cockroach strain (JM) were investigated. The JM strain originated from matings of the Munsyana (multiple resistance) strain and Johnson Wax (susceptible) strain. Two subpopulations of the JM strain were selected over three generations: one with a pyrethroid insecticide (cypermethrin) and one with an organophosphate insecticide (chlorpyrifos). Significant increases in resistance levels were observed in the first generation following selection. These trends continued for three generations and resistance levels to each insecticide approached those of the original Munsyana strain by the third generation of selection. Cypermethrin selected for cross-resistance to chlorpyrifos; however, chlorpyrifos selected for negative cross-resistance to cypermethrin. Increased body weight was weakly but positively correlated with increases in insecticide resistance to each insecticide. Examinations of metabolic enzymes indicated no change in total esterase (1-NA, 2-NA, and PNPA hydrolysis) or glutathione S-transferase (DCNB and CDNB conjugation) activity. Native PAGE of esterases identified one electromorph (E2) which stained more intensely following chlorpyrifos selection and which was inhibited by both chlorpyrifos and chlorpyrifosoxon. Examination of cytochromes P450 by carbon monoxide difference spectra indicated that each insecticide selected for increases in total cytochrome P450 content. However, in vitro demethylation and Western analysis results suggest that different cytochrome P450 isoforms were selected by each insecticide. (C) 1998 Academic Press.

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#### **Characterization of four microsatellite loci in tree weta (Orthoptera : Stenopelmidae): their potential usefulness for the study of Hemideina**

King, TM; Hanotte, O; Burke, T; Wallis, GP. 1998

#### **Factors affecting adult color polymorphism in the meadow grasshopper, *Conocephalus maculatus* (Orthoptera : Tettigoniidae)**

Oda, K; Ishii, M. 1998

To examine the factors regulating the adult color morph of the meadow grasshopper, *Conocephalus maculatus*, we carried out 2 series of experiments. In Series I? crosses between green and brown morphs were carried out to investigate the genetic effect. The percentage of green morphs in F1 hybrids between green females and green males was about 70% and the percentages in F-1 hybrids between parent pairs of different color morphs were significantly different. The results suggested that color polymorphism in *C. maculatus* was partly controlled by genetic factors. In Series II, the F1 hybrids were also reared under different conditions with respect to temperature, photoperiod, background color and relative humidity, to assess the effects on the proportion of color morphs. The body coloration of F1 hybrids was lighter and paler at 30 degrees C than at 25 degrees C, especially the brown morph, which shows that temperature affects the intensity of body color rather than color morph determination in adults.

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#### **Patterns of mating between two closely related ground crickets are not influenced by sympatry**

Gregory, PG; Remmenga, MD; Howard, DJ. 1998

*Allonemobius fasciatus* (De Geer) and *A. socius* (Scudder) (Orthoptera: Gryllidae) are small ground-dwelling crickets that meet and hybridize, to a limited extent, in a mosaic contact zone stretching from New Jersey to at least as far west as Illinois. To determine whether short-range signals such as visual cues, tactile stimulation, or pheromones are important in limiting gene flow between *A. fasciatus* and *A. socius* we carried out a study in the laboratory. A male or a female was placed in a cage with an *A. fasciatus* and *A. socius* individual of the opposite sex and the outcome, a conspecific or a heterospecific mating, was recorded. Overall, conspecific matings occurred more frequently than heterospecific matings. However, individuals from areas of sympatry were no more likely to mate with a conspecific than were individuals from areas of allopatry. Thus, the challenge posed by a related species has not resulted in a strengthening of positive assortative mating in these crickets.

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#### **Genetic linkage maps of the ground crickets *Allonemobius fasciatus* and *Allonemobius socius* using RAPD and allozyme markers**

Chu, JM; Howard, DJ. 1998

The ground crickets, *Allonemobius fasciatus* and *A. socius* are sister species and form a mosaic hybrid zone in the eastern United States. In this study, we developed RAPD markers and constructed genetic linkage maps for the two species, as a first step toward mapping quantitative trait loci that control conspecific sperm precedence. The *A. fasciatus* map consists of 25 markers mapped to 8 linkage groups, spanning 400.1 contiguous centiMorgans (cM). The average distance between



two framework markers is 23.5 cM. The *A. socius* map consists of 20 markers mapped to 6 linkage groups, spanning 400.5 contiguous cM. The average distance between two framework markers is 30.4 cM. A sex chromosome was identified in the *A. socius* map. These are the first reported genetic linkage maps for Orthoptera.

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#### Hybridization and geographic variation in two meadow katydid contact zones

Shapiro, LH. 1998

In this study, previously unrecognized hybridization was documented between two meadow katydids in each of two disjunct contact zones, in the southeastern United States and along the Potomac River near Washington, DC. These two zones have very different histories and dynamics of interaction between the two taxa. *Orchelimum nigripes* and *O. pulchellum* (Tettigoniidae: Conocephalinae) are distributed west and east, respectively, of the Appalachian Mountains, from the Great Lakes to the Gulf Coast and along the Atlantic Coastal Plain from New York to the Florida Keys, but are not found in the Appalachians themselves. In addition, during this century *O. nigripes* has become established in a small area east of the Appalachians, in the Potomac River basin, when it has completely replaced *O. pulchellum* along the river corridor above Washington, DC. I sampled katydids from 40 sites across both hybrid zones and mapped geographic patterns of genetic variation (allele frequencies at two diagnostic loci) and variation in a morphometric index for males. Although the two taxa are quite distinct over most of their extensive distributions, there is clear evidence of introgression in both contact zones. In the Deep South, samples from a transect along the Gulf Coast define a broad hybrid zone of about 50-100 km, while samples from a transect 200 km to the north define a zone of about 150-250 km in width. Only one Deep South population shows a deviation from Hardy-Weinberg equilibrium at either locus, and there is no evidence of linkage disequilibrium in any Deep South population. In the Potomac region, there is a narrow upstream-downstream hybrid zone along the river. Within the Potomac River floodplains downriver from Washington, DC, as well as outside the floodplains throughout the region, *O. pulchellum* is present in abundance, but *O. nigripes* markers are virtually absent. Within the floodplains upriver from Washington, DC, *O. nigripes* is abundant, but *O. pulchellum* markers are virtually absent. All four mixed ancestry Potomac populations sampled show strong and highly significant linkage disequilibrium, although only one clearly deviates from single-locus Hardy-Weinberg equilibrium. The position of the Deep South hybrid zone is generally consistent with interspecific and intraspecific phylogeographic patterns previously reported for numerous taxa from the southeastern United States. The observed genetic and morphometric differences appear to be the result of neutral introgression over thousands of years. In the much younger Potomac hybrid zone, *O. nigripes* appears to be spreading downriver, interbreeding with *O. pulchellum*, and replacing it. The mechanism for this replacement remains uncertain, but may be clarified by ongoing behavioral, genetic, and breeding studies.

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#### Genetic variation in cricket calling song across a hybrid zone between two sibling species

Mousseau, TA; Howard, DJ. 1998

The sibling ground crickets *Allonemobius fasciatus* and *A. socius* meet along a mosaic hybrid zone at approximately 40 degrees N latitude in eastern North America. In this paper we report the findings of a genetic analysis of calling-song variation within and among six cricket populations sampled along a transect through the hybrid zone in southern New Jersey. We compared aspects of the calling song of both wild-caught and laboratory-reared crickets to test the hypothesis that population differences in song observed in the wild were genetically based. We found significant, species-level differences in all aspects of the calling song, and these differences persisted even after a generation of common-garden rearing in the laboratory, supporting the hypothesis that interspecific variation observed in the wild largely reflects genetic differentiation between the two taxa. A discriminant function analysis indicated that individual crickets could be assigned to the proper taxon with less than 10% error, supporting the premise that calling song could be used by female crickets as a mechanism for species recognition. One population, collected from within the hybrid zone and containing significant numbers of hybrid individuals, was intermediate in its calling song, presumably reflecting this population's mixed genetic makeup. In this hybrid zone population, song phenotype was highly correlated to a hybrid index score generated using species-specific alleles at four diagnostic allozyme markers, suggesting a multigenic basis to calling-song variation in these crickets as well as linkage disequilibrium between markers and song. Based on an analysis of laboratory-reared full-sib families, broad-sense heritabilities for calling-song characteristics were generally significant in the two *A. socius* populations, whereas many components of song showed no significant family effects in the three *A. fasciatus* populations. The genotypically mixed, hybrid zone population showed very high heritabilities for most calling-song components, which likely reflect the influence of interspecific gene flow on genetic variation for quantitative traits.

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#### Mitochondrial DNA and phylogeography of the grasshopper *Trimerotropis pallidipennis* in relation to clinal distribution of chromosome polymorphisms

Confalonieri, VA; Sequeira, AS; Todaro, L; Vilardi, JC. 1998

*Trimerotropis pallidipennis* is an American grasshopper whose South American populations are polymorphic for pericentric inversions. Colonization of southern latitudes was by North American grasshoppers with basic chromosome arrangements, presumably along the Andean dry lands of South America. In Argentina, the frequencies of some of the rearrangements are correlated with geographical and climatic variables, following similar patterns among different ecological gradients, and are probably maintained by geographically variable coefficients of selection. Restriction site variation of mitochondrial DNA is used as a tool for determining the species history in relation to the formation of dines. Populations located along an altitudinal gradient, and others outside the dine, are analysed through phylogeographical studies. There is no strong geographical orientation in the unrooted tree connecting all 17 mitochondrial DNA haplotypes found. Many of them are present in most of the populations analysed, indicating high gene flow. The fact that there is no obvious differentiation in haplotype distribution between both extremes of the dine nor between chromosomally differentiated populations shows that the dine is not the result of a hybrid zone and reinforces the selection hypothesis. The estimation of the overall nucleotide divergence between the hypothetical ancestral haplotype and the other molecules shows that *T. pallidipennis* haplotypes started diverging from each other about 3 Myr ago. This result is in agreement with the time when the Isthmus of Panama rose (2-3 Myr ago), probably favouring the migration of many species between both hemispheres.

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#### Male sterility in interspecific meadow katydid hybrids

Cabrero, J; Shapiro, LH; Camacho, JPM. 1999

Spermatogenesis was cytologically analyzed in males of the conocephaline katydids *Orchelimum nigripes* and *O. pulchellum*, their hybrids obtained in the laboratory, and males from intermediate populations belonging to a broad hybrid zone. The results showed a very high similarity between the two species for the cytogenetic markers analyzed (C-heterochromatin content and location of nucleolus organizer regions), but artificial hybrids appeared to be completely sterile due to a complete absence of meiosis and spermatozoa in their reduced testes. *Orchelimum nigripes* and *O. pulchellum* are abundant and widespread conocephaline katydids found throughout much of the eastern United States. They are distributed west and east, respectively, of the Appalachian Mountains. Neither is known from the Appalachians themselves. South of the Appalachians, they form a very broad, and very old, hybrid zone, as evidenced by analysis of allozyme and morphological data. In addition, *O. nigripes* occurs east of the Appalachians along the Potomac River above Washington, D.C., where it has apparently been established for only 75 years or less and where it now forms a narrow hybrid zone with *O. pulchellum* (SHAPIRO 1998). There are no known differences between the calling songs of the two taxa, and in preliminary phonotaxis trials females showed no evidence of discriminating between the two (unpublished data). However, in laboratory mating trials using Potomac katydids, females of *O. nigripes* showed a strong preference for conspecific males when offered a choice between a male of each species (L. Shapiro, submitted), although in no-choice trials *O. nigripes* females mated freely with *O. pulchellum* males and produced normally viable offspring. The present study had two objectives. First, we wished to look for cytological markers that might be useful for the study of the *Orchelimum* hybrid zones. Second, we wished to analyze spermatogenesis and possible sterility of males collected from populations within the hybrid zone and hybrid males produced in the laboratory.

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## Chromosomal differentiation through an Alpine hybrid zone in the grasshopper *Chorthippus parallelus*

Flanagan, NS; Mason, PL; Gosálvez, J; Hewitt, GM. 1999

The grasshopper *Chorthippus parallelus* is genetically differentiated over its range into at least five major geographical subdivisions. Two of these subdivisions, designated as subspecies, meet and form a hybrid zone in the Pyrenees. These subspecies differ for a wide range of morphological, behavioural and chromosomal characters, which vary clinally across the zone. A further geographical subdivision exists within Italy. Here we present the first evidence for chromosomal divergence between populations of the grasshopper north and south of the Alps. Across two Alpine cols (Col de Larche, between France and Italy; Passe de Resia, between Austria and Italy), these populations differ in both structural and functional components of the X-chromosome. Northern Alpine individuals possess an active nucleolar organizing region (NOR) at the distal end of the X-chromosome and an associated region of heterochromatin (C-band). Both these features are absent from individuals from the south of the Alps. However, all individuals examined carry distally located rDNA on the X-chromosome. Clinal transition was examined in the distal C-band in transects through the two cols. The dine centres are roughly coincident with the tops of the cols. Both dines were of similar widths (Col de Larche, 21.88 km; Passe de Resia, 24.05 km), and therefore much wider than those for an X-Linked distal C-band in the Pyrenean hybrid zone. This suggests that there are different selective pressures on the cytogenetic characters in the Alps. The results are discussed in the context of the historical population dynamics of the species in relation to the climatic changes associated with the Pleistocene ice ages.

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## Reinforcement and other consequences of sympatry

Noor, MAF. 1999

The pattern of greater species mating discrimination between sympatric taxa than between allopatric taxa has been attributed to the strengthening of mate discrimination to avoid maladaptive hybridization. This process, termed reinforcement, has been highly contentious, particularly with regard to its role in speciation. Here, I review some recent studies of reinforcement, discuss alternative explanations for the pattern of greater species discrimination in sympatric taxa, and point to some new directions that may help to clarify the evolutionary forces involved. In particular, we need more ecological work on putative cases of reinforcement? more theoretical models that give diagnostic predictions of reinforcement relative to other modes of divergence, and empirical studies to evaluate these diagnostic predictions.

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## Reproductive costs to heterospecific mating between two hybridizing katydids (Orthoptera : Tettigoniidae)

Shapiro, LH. 2000

Animal taxa meeting in hybrid zones often exhibit partial reproductive isolation. This isolation may result from a variety of causes both before mating (e.g., incompatibilities in courtship behaviors) and subsequent to mating. Understanding the factors effecting reproductive isolation in hybrid zones can offer important insights into the process of speciation and the maintenance of species boundaries. The katydids *Orchelimum nigripes* Scudder and *O. pulchellum* Davis (Orthoptera: Tettigoniidae) form 2 hybrid zones in the eastern United States. I carried out breeding studies in the laboratory using animals from pure *O. nigripes* and *O. pulchellum* populations in the vicinity of one of these hybrid zones to examine possible modes of postmating reproductive isolation. The number of eggs produced by females mated to heterospecific males was dramatically lower than that of females mated conspecifically, but there was no evidence of any differences in hatch rate or offspring viability between egg clutches from heterospecific and conspecific crosses. Hatch rate, offspring viability, development time, and adult weight of hybrid progenies were all intermediate relative to corresponding values for progenies resulting from the 2 types of conspecific matings, although most of the differences between hybrids and each of the 2 classes of nonhybrid progenies were not statistically significant. The reduced oviposition of heterospecifically mated females suggests that females mated to heterospecific males do not receive the necessary stimulation to trigger oocyte maturation or oviposition behavior. The results reported here show that although some females will mate with heterospecific males, these matings tend to result in substantially reduced reproductive success relative to conspecific matings.

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## Pulse rates in the songs of trilling field crickets (Orthoptera : Gryllidae : Gryllus)

Walker, T.J. 2000

In cricket calling songs, pulse rate is often the feature that allows females to home on the songs of conspecific males while ignoring those of other species. A previous study of the sibling species *Gryllus rubens* Scudder and *G. texensis* Cade & Otte from western Florida showed unexpected effects of developmental conditions and parental generation on the pulse rates of their songs. The current study tested for these and other effects in *G. rubens* from Gainesville, FL, and *G. texensis* from Dallas, TX. In both species, sibships from different field-fertilized females differed significantly in the effects of rearing environment on the pulse rates of their songs. Tests for effects of nymphal diapause and adult age were negative. Hybrids between the two species produced pulse rates intermediate to the rates of the control crosses. Males of *G. rubens* reared at 32 degrees C produced faster pulse rates (at a standard temperature) than those reared at 25 degrees C. Furthermore, pulse rates of field-collected males in this study and of field-collected and laboratory-reared males in the previous study increased in rough proportion to the known and estimated temperatures during nymphal development.

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## Robertsonian translocations and B chromosomes in the Wellington tree weta, *Hemideina crassidens* (Orthoptera : Anostomatidae)

Morgan-Richards, M. 2000

Two karyotypes within the species *Hemideina crassidens* are described,  $2n = 15$  (XO) and  $2n = 19$  (XO). These two karyotypes have a NF of 28. The 19-karyotype was found exclusively in the southern part of the species range and the 15-karyotype was found in the north. The differences between the two karyotypes are interpreted as arising from two Robertsonian translocations (fission/fusion). Laboratory matings between weta with the two karyotypes produced viable offspring. During meiosis in F-1 intraspecific hybrids metacentric and acrocentric autosomes aligned to form two trivalents, confirming homologies predicted by Robertsonian translocations. The subspecies *H. c. crassiciuris*, (confined to Stephens Island) was found to be polymorphic for a metacentric B chromosome. An unusual association of sex and presence of B chromosome was observed in this island population with Bs found only in male weta.

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## Inferring the patterns and causes of geographic variation in *Ephippiger ephippiger* (Orthoptera, Tettigoniidae) using geographical information systems (GIS)

Kidd, DM; Ritchie, MG. 2000

*Ephippiger ephippiger* is a tettigoniid cricket that is fairly widespread in Europe. In southern France, between the Alps and the Pyrenees, it is geographically highly variable for a number of different traits including morphology, allozymes, behaviour and genetic markers. This variation has resulted in considerable confusion over the taxonomic and evolutionary status of forms of the organism. Through the use of geographical information systems (GIS) it has been possible to integrate both

trail and environmental data sets from a variety of sources. The GIS is used to interpolate trait and environmental surfaces that are then examined for coincidence. Four general spatial patterns are identified. These can be explained through a combination of secondary contact, environmental adaptation and drift. Covariance between trait and environmental surfaces point to patterns which are primary in origin, whereas other clines probably reflect secondary contact following divergence in refugia. Multivariate statistics support the validity of a major subdivision identified by GIS. This study is an example of the considerable potential for GIS as an investigative tool in evolutionary studies. (C) 2000 The Linnean Society of London.

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#### **The spheroidin of an Entomopoxvirus isolated from the grasshopper *Anacridium aegyptium* (AaEPV) shares low homology with spheroidins from lepidopteran or coleopteran EPVs**

Hernandez-Crespo, P; Veyrunes, JC; Cousserans, F; Bergoin, M. 2000

Based on virion morphology, the current virus taxonomy groups entomopoxviruses (EPVs) (Poxvirus: Entomopoxvirinae) from coleopteran and dipteran hosts in separated genera, whilst it keeps viruses infecting either lepidopteran or orthopteran hosts in the same genus. In contrast to the morphological criteria, the few data available from recent studies at the genetic level have suggested that EPVs infecting different insect orders are phylogenetically distant. In order to elucidate EPVs phylogeny we have cloned and sequenced the highly conserved/highly expressed spheroidin gene of *Anacridium aegyptium* entomopoxvirus (AaEPV). This gene and its promoter is of interest for the development of genetic engineering on EPVs. The spheroidin gene was located in the AaEPV genome by Southern blot and hybridisation with specific degenerated oligonucleotide probes synthesised after partial sequencing of the purified spheroidin protein. A total of 3489 bp were sequenced. This sequence included the coding and promoter region of 969 residues 108.8 kDa protein identified as spheroidin. AaEPV spheroidin contains 21 cysteine residues (2.2%) and 14 N-glycosylation putative sites distributed along the sequence. The cysteine residues are particularly abundant at the C-terminal end of the protein, with 11 residues in the last 118 aa. Our results confirm that the spheroidin is highly conserved only between EPVs isolated from the same insect order. Polyclonal antibodies raised against AaEPV spherules specifically revealed spheroidin in Western Blots failing to cross-react with MmEPV or AmEPV spheroidins or MmEPV fusolin. Comparison of spheroidins at the aa level demonstrate that AaEPV spheroidin shares only 22.2 and 21.9% identity with the lepidopteran AmEPV and the coleopteran MmEPV spheroidins, respectively, but 82.8% identity with the orthopteran MsEPV spheroidin. Only two highly conserved domains containing the sequence (V/Y)NADTG(C/L) and LFAR(I/A) have been identified in all known spheroidins. The phylogenetic tree constructed according to the CLUSTALX analysis program revealed that EPVs are clearly separated in three groups - lepidopteran, coleopteran and orthopteran - according to the insect order of the virus hosts. In base to our results, the split of the genus Entomopoxvirus B dissociating lepidopteran and orthopteran EPVs into two different genera is suggested. (C) 2000 Elsevier Science B.V. All rights reserved.

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#### **Characterization of a hybrid zone between two chromosomal races of the weta *Hemideina thoracica* following a geologically recent volcanic eruption**

Morgan-Richards, M; Treweek, SA; Wallis, GP. 2000

Two chromosomal races ( $2n = 17$  and  $2n = 15$ , XO) of the weta *Hemideina thoracica* meet at the centre of a volcanic region in North Island, New Zealand. Five independent polymorphic genetic markers showed broadly coinciding, steep frequency cline from north to south across this zone beside the flooded crater, Lake Taupo. Three unlinked nuclear gene markers provide estimates of zone width that are at least twice the width of the chromosomal and mitochondrial clines, with cline centres displaced at least 2.5 km. The different zone widths and centres suggest that this hybrid zone is a semipermeable barrier reducing the introgression of the chromosomal markers more than genic markers. We estimate that this species of weta must have a dispersal rate of at least 100 m per generation using the time since the last Taupo eruption (1850 years ago), which covered an area of about 20 000 km<sup>2</sup> with pyroclastic flow.

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#### **Chromosome polymorphism and C-banding variation of the brachypterous grasshopper *Podisma sapporensis* Shir. (Orthoptera, Acrididae) in Hokkaido, northern Japan**

Bugrov, AG; Warchalowska-Sliwa, E; Tatsuta, H; Akimoto, S. 2001

The grasshopper *Podisma sapporensis* consists of two main chromosome races in Hokkaido. The western group of populations of *P. sapporensis*, belonging to the XO race, has a diploid number of chromosomes  $2n=23$  in the male and  $2n=24$  in the female (sex determination XO male/XX female). The eastern group of populations of this species, belonging to the XY race, differs from the western one as a result of Robertsonian translocation between the originally acrocentric X chromosome and M-5 autosome in homozygous state, having resulted in the forming of chromosome sex determination neo-XY male/neo-XX female ( $2n=22$ ). These races are geographically isolated by the mountainous system consisting of the Mts Daisetsu and Hidaka range, occupying the central part of the island. The hybrid zones between the races have not so far been discovered. Various levels of polymorphism for the pericentric inversions and C-banding variation exist in different chromosomes throughout populations in both chromosome races. In some solitary populations (the population at the summit of Mt Yotei, populations in the vicinity of Naganuma, Oketo, and Tanno) pericentric inversions are fixed in some pairs of chromosomes, which enables marking of the discrete karyomorphs. In the Mt Daisetsu population all chromosomes are two-armed as a result of fixing the pericentric inversions. These facts contradict karyotypic conservatism of the tribe Podimini. The level of diversity of *P. sapporensis* karyotypes could provide a new perspective on the evolutionary process of different karyotype in Orthoptera. The considerable occurrence of polymorphism in chromosomes suggests that karyotypic diversification is undergoing in *P. sapporensis*. The authors also proposed that *P. sapporensis* would be divided into four chromosome subraces in the XO chromosome race and two chromosome subraces in the XY race, on the basis of karyotypic features. These races may have been established by fundamental climatic changes during the glacial epoch.

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#### **Asymmetric assortative mating between two hybridizing *Orchelimum* katydids (Orthoptera : Tettigoniidae)**

Shapiro, LH. 2001

The katydids *Orchelimum nigripes* and *O. pulchellum* (Orthoptera: Tettigoniidae) have a largely allopatric distribution in the eastern United States, but hybridization between these species has been well documented in two contact zones. I used animals from populations just outside a narrow, recently formed upstream-downstream hybrid zone along the Potomac River near Washington, D.C., in laboratory mate-choice trials to examine the possible importance of differential patterns of mate preference in determining the structure and dynamics of this hybrid zone. Offered a choice between a male of each species, *O. nigripes* females showed an extreme preference for conspecific mates, but *O. pulchellum* females showed no clear preference. This asymmetry in mate discrimination may contribute to the apparently ongoing replacement along the Potomac of *O. pulchellum* by *O. nigripes* in the wake of a moving hybrid zone.

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#### ***Gryllus cayensis* n. sp (Orthoptera : Gryllidae), a taciturn wood cricket extirpated from the Florida Keys: Songs, ecology and hybrids**

Walker, TJ. 2001

*Gryllus cayensis*, new species, formerly occurred in tropical hammocks in the Florida Keys but has not been found there since 1972, the initial year of aerial spraying of north Key, Largo hammocks for mosquito control. It is now known only from pineland in Everglades National Park. Males of *G. cayensis* make no ordinary calling songs, but some caged males occasionally produce soft 3-4 pulse chirps with a principal frequency of nearly 11 kHz. Males of its sister species, *G. fultoni* (Alexander), which occurs in north Florida, call with loud 2-4 pulse chirps with a principal frequency of about 4.5 kHz.

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## Two new grasshopper species in the texanus group of the genus *Melanoplus* (Orthoptera : Acrididae : Melanoplineae) with biological notes on the group

Hilliard, JR. 2001

*Melanoplus alexanderi* n. sp. from South-Central Texas Counties centered around Bastrop County and *Melanoplus dakini* n.sp. from west central Louisiana are described. These two short wing species are part of the 7 member allopatric *Melanoplus texanus* species group. Distinguishing structure, distribution, habitat, food preferences and egg pods are described and compared. Evidences for hybridization between *Melanoplus warneri*, having the neo-XY + 10 pairs autosomes karyotype, and *Melanoplus angularis*, having the XO + 11 pairs of autosomes karyotype, are noted. Characteristics of populations of intergrades between *Melanoplus angularis* and *Melanoplus dakini* in four far southeast Texas (Jasper, Newton, Sabine and San Augustine Counties) are delineated.

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## Spatial structure and habitat variation in a grasshopper hybrid zone

Bridle, JR; Baird, SJE; Butlin, RK. 2001

A hybrid zone between the grasshoppers *Chorthippus brunneus* and *C. jacobsi* (Orthoptera: Acrididae) in northern Spain has been analyzed for variation in morphology and ecology. These species are readily distinguished by the number of stridulatory pegs on the hind femur. Both sexes are fully winged and inhabit disturbed habitats throughout the study area. We develop a maximum-likelihood approach to fitting a two-dimensional cline to geographical variation in quantitative traits and for estimating associations of population mean with local habitat. This method reveals a cline in peg number approximately 30 km south of the Picos de Europa Mountains that shows substantial deviations in population mean compared with the expectations of simple tension zone models. The inclusion of variation in local vegetation in the model explains a significant proportion of the residual variation in peg number, indicating that habitat-genotype associations contribute to the observed spatial pattern. However, this association is weak, and a number of populations continue to show strong deviations in mean even after habitat is included in the final model. These outliers may be the result of long-distance colonization of sites distant from the cline center or may be due to a patchy pattern of initial contact during postglacial expansion. As well as contrasting with the smooth hybrid zones described for *Chorthippus parallelus*, this situation also contrasts with the mosaic hybrid zones observed in *Gryllus* crickets and in parts of the hybrid zone between *Bombina* toad species, where habitat-genotype associations account for substantial amounts of among-site variation.

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## Spatio-temporal dynamics of the *Allonemobius fasciatus*-*A. socius* mosaic hybrid zone: a 14-year perspective

Britch, SC; Cain, ML; Howard, DJ. 2001

Long-term studies of hybrid zones can provide valuable insight into a number of questions that have long attracted the attention of evolutionists. These questions range from the stability and fate of hybrid zones to the relative fitness of hybrids. In this paper we report the results of a 14-year survey of the *Allonemobius fasciatus*-*Allonemobius socius* hybrid zone. Populations were collected intensively in 1986 and 1987 and then more sporadically through the end of the 1980s and throughout the 1990s. By documenting changes in the genetic composition of populations near and within the zone during this period of time we assessed: the strength of the reproductive isolation between the two species; the relative growth rates (which can be considered a surrogate of relative fitness) of genotype classes corresponding to hybrids and to pure species individuals; and, the power of single-year and multi-year measurements of relative growth rates to predict changes in the genetic composition of mixed populations through time. In brief, we found very large year-to-year variation in the relative growth rates of pure species and hybrid individuals. This variation may reflect the fact that both species are at the edge of their range and perhaps at the limits of their ability to deal with environmental perturbations. As a consequence of the variation, even multi-year estimates of relative growth rates often provided imprecise predictions regarding the future genotypic composition of mixed populations. Despite our limited ability to predict the dynamics of individual populations, some trends are apparent. *A. socius*, the southern species, has clearly increased in frequency along a transect through the Appalachian Mountains, indicating that the zone is moving north in this region. In contrast, the zone appeared to be more stable along the East Coast transect. Within mixed populations, character-index profiles are often bimodal and stable through time, indicating relatively strong reproductive isolation between the two species that is not being reinforced, nor is it breaking down.

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## Mating signal variation and bimodality in a mosaic hybrid zone between *Chorthippus* grasshopper species

Bridle, JR; Butlin, RK. 2002

The grasshoppers *Chorthippus brunneus* and *Chorthippus jacobsi* are easily distinguished by male calling song and the number of stridulatory pegs on the hind femur, and form a mosaic hybrid zone in northern Spain. In this paper, we fit a two-dimensional cline to variation in male calling song characters, which are of particular interest as they are likely to be involved in mate choice by females. As with variation in peg number, local habitat makes only a small contribution in explaining deviations in mean song score from clinal expectations. However, the fitted width of the cline for song characters is significantly narrower than for peg number, suggesting that mating signals may be associated with reduced hybrid fitness in the field and that recombination rates are sufficient to allow clines for different characters to diverge in width. Despite this, estimates for the overall elevation in linkage disequilibrium at the zone center, based on covariance between peg and song characters, reveal a substantial overrepresentation of parental genotypes at the cline center relative to the expectations of a tension zone of similar width. Examination of covariance at individual sites reveals that this inflated estimate of linkage disequilibrium is caused by several sites where the distribution of phenotypes is effectively bimodal. This substantial variation in linkage disequilibrium at the cline center could result from local variation in the strength of assortative mating or selection against hybrids, or may reflect the long-distance colonization of empty habitat from outside the hybrid zone, which would continually create new contacts between parental genotypes at the cline center. Hybrid zones like this, in which strong, linkage disequilibrium occurs in some situations but not in others, are of particular relevance to speciation research and allow investigation of the spread of combinations of alleles through different genetic and ecological backgrounds.

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## Fine-scale ecological and genetic variation in a *Chorthippus* grasshopper hybrid zone

Bridle, JR; Vass-De-Zomba, J; Butlin, RK. 2002

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## A comparison of five hybrid zones of the weta *Hemideina thoracica* (Orthoptera : Anostostomatidae): Degree of cytogenetic differentiation fails to predict zone width

Morgan-Richards, M; Wallis, GP. 2003

Tension zones are maintained by the interaction between selection against hybrids and dispersal of individuals. Investigating multiple hybrid zones within a single species provides the opportunity to examine differences in zone structure on a background of differences in extrinsic factors (e.g., age of the zone, ecology) or intrinsic factors (e.g., chromosomes). The New Zealand tree weta *Hemideina thoracica* comprises at least eight distinct chromosomal races with diploid numbers ranging from  $2n = 11$  (XO) to  $2n = 23$  (XO). Five independent hybrid zones were located that involve races differing from one another by a variety of chromosomal rearrangements. The predicted negative correlation between extent of karyotypic differentiation (measured in terms of both percent of genome and number of rearrangements) and zone width was not found. Conversely, the widest zones were those characterized by two chromosome rearrangements involving up to 35% of

the genome. The narrowest zone occurred where the two races differ by a single chromosome rearrangement involving approximately 2% of the genome. The five estimates of chromosomal cline width ranged from 0.5 km to 47 km. A comparative investigation of cline width for both chromosomal and mitochondrial markers revealed a complex pattern of zone characteristics. Three of the five zones in this study showed cline concordance for the nuclear and cytoplasmic markers, and at two of the zones the clines were also coincident. Zones with the widest chromosomal clines had the widest mitochondrial DNA clines. It appears that, even within a single species, the extent of karyotypic differentiation between pairs of races is not a good predictor of the level of disadvantage suffered by hybrids.

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#### Transitions in cuticular composition across a hybrid zone: historical accident or environmental adaptation?

Buckley, SH; Tregenza, T; Butlin, RK. 2003

Two subspecies of the grasshopper *Chorthippus parallelus* form a hybrid zone in the Pyrenees. Transitions across the zone, including changes in mating signals and reproductive isolation have been intensively studied. Cuticular pheromones have been identified as likely mate recognition signals. Since the major role of the cuticle is in waterproofing, environmental adaptation of cuticular composition has the interesting potential to generate assortative mating as an incidental by-product. We describe the pattern of variation in cuticular hydrocarbon blend in four transects through the hybrid zone. We find no evidence for a previously observed displaced cline in one blend component. There were differences between subspecies but these varied among transects and were small compared with variation between transects. We examined environmental variation within one transect and found a correlation between vegetation and cuticular composition, suggesting that environment influences the constitution of the cuticle, and hence natural selection may interact with mating signals in this species. (C) 2003 The Linnean Society of London.

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#### Complex courtship in a bimodal grasshopper hybrid zone

Vedenina, VY; von Helversen, O. 2003

Grasshoppers of the *Chorthippus albomarginatus*-group, which is outstanding with respect to its complex courtship song, were studied at fifteen localities in the Ukraine and Moldova. The analysis of the courtship songs revealed two species: *C. albomarginatus* in northeastern Ukraine and *Chorthippus oschei* in the southwestern Ukraine and Moldova. In a belt about 200 km wide, not only were one or the other pure species found, but also males with intermediate song characters. *C. albomarginatus* and *C. oschei* were hybridised in the laboratory, and F1 hybrid males as well as F2 hybrid males produced intermediate song patterns, quite similar to those recorded in the field. We defined a "hybrid song score" for intermediate songs. The score showed a bimodal distribution with most songs resembling one or other parental type, but with only a few intermediates. At several localities, where hybrids with songs similar to one of the parental species dominated, some individual males sang more similarly to the other species. In one locality, two hybrid populations only 3 km apart had different parental types. Hybrid songs can contain novel elements, even more complex than the parental ones, which may offer a new starting point for sexual selection. We suggest that genetic introgression occurs between the two sibling species *C. albomarginatus* and *C. oschei* within a wide hybrid zone stretching over a distance of several hundred kilometres, but with a patchy spatial distribution.

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#### Phylogeographic genetic analysis of the alpine weta, *Hemideina maori*: evolution of a colour polymorphism and origins of a hybrid zone

King, TM; Kennedy, M; Wallis, GP. 2003

Body colour is an important distinguishing feature in a New Zealand alpine weta hybrid zone and is strongly correlated with mitochondrial DNA haplotype variation. To assess the broader geographic pattern of this association, an intraspecific phylogeny was generated using mtDNA sequence. Both parsimony and likelihood analyses separated the colour morphs into two clades. One grouped the Rock and Pillar Range "yellow" haplotypes with other Central Otago populations and the other grouped the "black" Rock and Pillar haplotypes as a monophyletic group. The black body colour seen in the south of the Rock and Pillar Range appears to have evolved multiple times across the species. Application of a molecular clock estimated that the Rock and Pillar yellow and black lineages were separated approximately 2 million years ago. The Rock and Pillar yellow lineage split from other Central Otago populations approximately 1 million years later, possibly the result of sequential range contraction and expansion.

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#### The evolution of insect mating structures through sexual selection

Siro, LK. 2003

Mating structures are of interest to a wide range of biologists because, in many taxa, mating structures are incredibly diverse and range widely in elaboration even between closely related species. As a result of this diversity, mating structures have been useful in species identification. Historically, the evolution of diverse mating structures has been attributed to post-zygotic selection for pre-zygotic isolation to avoid production of hybrid offspring. More recently, sexual selection has been proposed as an alternative explanation for the rapid diversification of mating structures. Mating structures could diversify between populations through sexual selection if sexual selection acted differently on mating structures in different populations. Eberhard (1985) wrote a comprehensive book explaining how sexual selection could result in the diversification of mating structures and providing examples to support the hypothesis, but none of the examples were experimental tests of the hypothesis. Since 1985, a few studies have experimentally tested this hypothesis. However, there have been no empirical studies that connect intraspecific selection with interspecific diversification. In this paper, I review the reproductive isolation and sexual selection hypotheses and two recent experimental tests of the sexual selection hypothesis. Then, I provide a description of a system that may allow one to establish a connection between sexual selection on mating structures within a species and diversification of mating structures between species.

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#### Premating barriers to gene exchange and their implications for the structure of a mosaic hybrid zone between *Chorthippus brunneus* and *C. jacobsi* (Orthoptera : Acrididae)

Bailey, RI; Thomas, CD; Butlin, RK. 2004

Many hybrid zones contain a deficit of hybrid genotypes relative to expectations from tension zone models. This is often associated with separation of parental genotypes into distinct habitats (mosaicism), but sometimes parentals can be found co-occurring in the same local population (bimodality). In both cases, prezygotic isolation may play an important role in determining the genotypic composition of the zone. *Chorthippus brunneus* and *C. jacobsi* (Orthoptera: Acrididae) meet and form a complex hybrid zone in northern Spain. Analysis of stridulatory peg numbers reveals partial spatial and seasonal isolation in a 25 km<sup>2</sup> area of the zone: *C. jacobsi* phenotypes predominate in June and July and are present in both valley and mountain habitats; *C. brunneus* phenotypes predominate in August and are restricted to valley habitats, always in sympatry with *C. jacobsi*. Strong assortative mating was observed in laboratory mating experiments. Spatial, seasonal and behavioural isolation combine to produce strong premating isolation in the study area. These results suggest a role for premating isolation in maintaining both the mosaic structure and bimodality of this hybrid zone.

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## Experimental hybridisation between X0 and XY chromosome races in the grasshopper *Podisma sapporensis* Shir. (Orthoptera, Acrididae). I. Cytological analysis of embryos and F1 hybrids

Bugrov, AG; Warchalowska-Sliwa, E; Sugano, Y; Akimoto, S. 2004

The results of experimental hybridisation between some chromosome subraces belonging to the X0 and XY chromosome races of the brachypterous grasshopper *P. sapporensis* are presented. Pre-zygotic reproductive isolation mechanisms in experimental pairs were not confirmed. In crossings of XY-standard x X0-standard and XY-standard x X0-Naganuma chromosome subraces, a zygotic barrier has been found. All embryos of XY-standard x X0-standard crosses and the vast majority of embryos of XY-standard x X0-Naganuma crosses were obtained from female diploid or haploid/diploid cells as a result of parthenogenesis. In very rare cases, when the zygotic barriers had been surmounted, normal embryo heterozygotes and a F1 hybrid generation were obtained in XY-standard x X0-Naganuma crosses. On the contrary, crosses between the XY-Tanno and X0-standard subraces gave viable offspring in spite of many chromosome differences such as a X-A translocation and fixed pericentric inversions in four pairs of autosomes. The results obtained do not support the hypothesis that chromosomal differences play a key role in restricting gene flow between X0 and XY races of *P. sapporensis*. The presence of crossing barriers explains the phenomena of the purity of the X0 and XY chromosomes races.

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## Genetic differentiation of *Loxoblemmus appendicularis* complex (Orthoptera : Gryllidae): Speciation through vicariant and glaciation events

Yeh, WB; Chang, YL; Lin, CH; Wu, FS; Yang, JT. 2004

Taxonomic determination based on morphology alone has failed to describe the evolutionary history of *Loxoblemmus appendicularis* Shiraki complex in Taiwan. Phylogenetic analysis using the 16S rDNA sequence reveals that three evolutionary lineages of *L. appendicularis* have been found to coincide with their area of geographical distribution: the Southern, Eastern, and Northern Populations. Sequence distance was equal between the Northern and Southern and Northern and Eastern Populations (0.032), whereas between the Southern and Eastern Populations, the sequence distance was 0.026. Cross-breeding among these three populations has produced abnormal hybrids, suggesting that a possible postzygotic isolating mechanism exists. Biogeographical history suggests the speciation event in *L. appendicularis* began in the early Pleistocene (1.8 million yr ago [Mya]). Vicariant event created by the rise of the Central Mountain Range >1 Mya led to two separate Eastern and Southern lineages. The following glacial event and formation of a land bridge between Taiwan and the Chinese continent at the end of Pleistocene reintroduced *L. appendicularis*, currently known as the Northern population, to western and northern Taiwan. Results of sequence divergence, phylogenetic inferences, geographical distribution, and cross-breeding strongly show a current taxonomic recognition of a single species with three parapatric cryptic species.

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## Do suture zones exist?

Swenson, NG; Howard, DJ. 2004

Remington (1968) argued that 13 suture zones exist in North America. Remington defined a suture zone as, "a band of geographic overlap between major biotic assemblages, including some pairs of species or semispecies which hybridize in the zone" (p. 322). Although initially controversial, the idea that suture zones exist has picked up momentum over the past decade, due largely to the phylogeographic work of Hewitt, A vise, and their colleagues. Nevertheless, the reality of suture zones has not yet been subjected to rigorous analysis using statistical and geographic information system (GIS) approaches. To test for the existence of Remington's suture zones, we first identified 117 terrestrial hybrid zones in Canada and the United States through a literature search for the key words "cline," "contact zone," "hybrid zone," and "hybridization" in articles published between 1970 and 2002. The 117 hybrid zones were mapped using a GIS approach and compared with a digitized version of Remington's original suture zone map. Overall, there does appear to be an association between hybrid zones and suture zones, but this association is largely attributable to clustering of hybrid zones in only two of the 13 suture zones recognized by Remington. The results suggest that evolutionary biologists should retain some skepticism toward Remington's suture zones.

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## Cricket song in sympatry: Species specificity of song without reproductive character displacement in *Gryllus rubens*

Izzo, AS; Gray, DA. 2004

Previous work with the cryptic sister species pair of field crickets, *Gryllus texensis* Cade & Otte and *Gryllus rubens* Scudder, has implicated sexual selection in the speciation process. That study examined reproductive character displacement (RCD) in male song and female preference for song in *G. texensis*. No evidence of RCD was found. Here, we provide a similar analysis of RCD in *G. rubens* song and examine the songs of both species from areas of sympatry in an effort to document the species-specificity of song in sympatry and to look for individuals with songs indicative of F1 hybrid status. We 1) find no evidence for RCD in *G. rubens* song, 2) demonstrate the distinctness of song in sympatry, and 3) document the rarity of songs typical of F1 hybrids.

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## Systematics and bioacoustics of the *Poecilimon sanctipauli*-group (Orthoptera : Tettigoniodea : Phaneropteridae)

Heller, KG; Sevgili, H. 2005

In this paper a combination of characters by which *Poecilimon* species (Orthoptera: Tettigoniodea: Phaneropteridae) can be recognised as members of the *P. sanctipauli* group are described. Most important are the wide fastigium, short ovipositor and song characters. The morphological characters are figured and described (Table 1), and the song patterns illustrated by oscillograms. The proposed phylogenetic relationships or the members of this group are written as [*P. mytilenensis* (*P. pulcher*, *P. lodosi*, *P. sanctipauli*)]. All species of the group are known from southwest Turkey and some east Aegean islands. The three species *P. pulcher*, *P. lodosi* and *P. sanctipauli* are morphologically and bioacoustically quite similar. *P. sanctipauli* and *P. pulcher* are distinct species. *P. lodosi*, however, possesses a combination of the key characters of the other two species. It may be a relict species or, in our opinion more probably, a species of hybrid origin.

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## The secondary copulatory organ in female ground weta (*Hemiandrus pallitarsis*, Orthoptera : Anostostomatidae): a sexually selected device in females?

Gwynne, DT. 2005

Secondary sexual devices in female insects, primarily abdominal modifications, appear to function as a means of thwarting coercive mating attempts by males or are, in rare cases, sexually selected adaptations. Female ground weta, *Hemiandrus pallitarsis* (Orthoptera: Anostostomatidae), have an elaborate elbowed device on the underside of the mid-abdomen. Experimental removal of this accessory organ shows that it does not increase the probability of mating as predicted by the thwart-copulation hypothesis. Instead, removal prevents copulation, thus demonstrating that it is a secondary copulatory device. The male attaches to the organ both at the beginning of copulation and at the end, when he positions himself to adhere a spermatophylax food gift onto the mid-ventral region of his mate. The female accessory organ does not function to manipulate eggs or larvae (females provide care to their single clutch of offspring) and is unlikely to be a copulatory structure that prevents hybridization. The great extent of the modification of the ventral abdominal segments of *H. pallitarsis* females compared to other *Hemiandrus* species is consistent with a history of sexual selection on the accessory organ. Taken together, these results and the finding that the length of the accessory organ of *H. pallitarsis* correlates with female fecundity, suggest that this structure evolved under sexual selection to acquire nuptial gifts from males. (c) 2005 The Linnean



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#### Hybrids between *Chorthippus brunneus* and *C-jacobsi* (Orthoptera : Acrididae) do not show endogenous postzygotic isolation

Saldamando, CI; Tatsuta, H; Butlin, RK. 2005

Studies of prezygotic and postzygotic isolation in *Drosophila* have shown in general that species in sympatry tend to evolve prezygotic barriers earlier than do species in allopatry. However, postzygotic barriers tend to evolve at the same evolutionary rate in both sympatric and allopatric species. In contrast to these observations, the grasshoppers *Chorthippus parallelus parallelus* and *C. p. erythropus* show complete hybrid male sterility but only limited prezygotic isolation after an estimated 0.5 millions years of divergence. Like their congeners, *C. brunneus* and *C. jacobsi* form a hybrid zone where their ranges meet in northern Spain. However, the hybrid zone is mosaic and bimodal and, in contrast to the high levels of postzygotic isolation between *C. parallelus* subspecies, these two species showed no significant reduction in hybrid fitness in F<sub>1</sub> or backcross generations relative to the parental generations. The level of prezygotic isolation in laboratory tests was comparable to that between *C. parallelus* subspecies. These results suggest that endogenous postzygotic isolation does not play an important role in the reproductive isolation between *C. brunneus* and *C. jacobsi*, or in determining the structure of the hybrid zone. Exogenous postzygotic isolation may be present and should be tested in future studies. (C) 2005 The Linnean Society of London.

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#### Inheritance of song and stridulatory peg number divergence between *Chorthippus brunneus* and *C-jacobsi*, two naturally hybridizing grasshopper species (Orthoptera : Acrididae)

Saldamando, CI; Miyaguchi, S; Tatsuta, H; Kishino, H; Bridle, JR; Butlin, RK. 2005

Knowledge of the genetic basis of divergence in mating signal characters that contribute to reproductive isolation is critical to understanding speciation. Here, we describe a semi-automated system for characterizing grasshopper acoustic signals. We used this system to study the genetic basis of divergence in three male calling song components [echeme (EL), syllable (SL) and phrase (PL) lengths] between *Chorthippus brunneus* and *C. jacobsi*, two species of grasshoppers that hybridize in northern Spain. We also studied the number of pegs in the stridulatory file. For all characters, additive effects accounted for most of the genetic differentiation between species. However, the three song components also showed small but significant epistatic effects. No sex linkage was detected. Wright-Castle-Lande estimates of the minimum numbers of genetic factors underlying song and peg number divergence were low: peg number ( $n(e) = 5.87 \pm 5.84$ ), SL ( $n(e) = 2.37 \pm 4.79$ ) and PL ( $n(e) = 0.87 \pm 0.86$ ). On the other hand, EL appeared to be controlled by many genes. These results suggest that divergence in SL and PL might be driven by sexual selection whereas EL might not be under selection. This is consistent with experimental results on female song preference in related species. However, the fact that few factors appear to underlie the differences in peg number is surprising. Peg number is not closely related to song characteristics. It often varies between closely related grasshopper species and it has been assumed to be a neutral character. The biometrical approaches used here tend to underestimate the number of factors influencing a trait but provide valuable background for subsequent quantitative trait loci analyses.

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#### Hybrid origin of a parthenogenetic genus?

Morgan-Richards, M; Trewick, SA. 2005

The origin of the obligate-parthenogenetic New Zealand stick insect genus *Acanthoxyla* was investigated using cytogenetics and sequencing of nuclear and mitochondrial DNA. Little mitochondrial DNA sequence variation (COI-II) was found among seven species of the genus *Acanthoxyla* and we found no evidence for monophyly of the morphologically distinguished lineages. In contrast, two distinct clades of nuclear sequence (ITS) were obtained, one is restricted to the genus *Acanthoxyla*, while the other includes sequences obtained from its sister genus *Clitarchus*. Although *Acanthoxyla* appears to be diploid ( $2n = 36-38$ ), it has two ill-matched chromosome pairs. We hypothesize that two or more hybridization events involving the parental sexual species *Clitarchus hookeri* and an unknown taxon probably resulted in the formation of the parthenogenetic genus *Acanthoxyla*. However, the karyotype of *Acanthoxyla* bears little resemblance to the karyotype of the putative paternal species *C. hookeri* so the exact nature of *Acanthoxyla* remains in question.

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#### Patterns of male sterility in a grasshopper hybrid zone imply accumulation of hybrid incompatibilities without selection

Shuker, DM; Underwood, K; King, TM; Butlin, RK. 2005

It is now widely accepted that post-zygotic reproductive isolation is the result of negative epistatic interactions between derived alleles fixed independently at different loci in diverging populations (the Dobzhansky-Muller model). What is less clear is the nature of the loci involved and whether the derived alleles increase in frequency through genetic drift, or as a result of natural or sexual selection. If incompatible alleles are fixed by selection, transient polymorphisms will be rare and clines for these alleles will be steep where divergent populations meet. If they evolve by drift, populations are expected to harbour substantial genetic variation in compatibility and alleles will introgress across hybrid zones once they recombine onto a genetic background with which they are compatible. Here we show that variation in male sterility in a naturally occurring *Chorthippus parallelus* grasshopper hybrid zone conforms to the neutral expectations. Asymmetrical clines for male sterility have long tails of introgression and populations distant from the zone centre show significant genetic variation for compatibility. Our data contrast with recent observations on 'speciation genes' that have diverged as a result of strong natural selection.

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#### Fewer species of *Argosarchus* and *Clitarchus* stick insects (Phasmida, Phasmatinae): evidence from nuclear and mitochondrial DNA sequence data

Trewick, SA; Goldberg, J; Morgan-Richards, M. 2005

The systematics of three genera of New Zealand stick insect in the subfamily Phasmatinae were investigated in light of inconsistencies in morphological variability within and among species. We sequenced a region of the mitochondrial genome, cytochrome oxidase (COI & COII; 1448 bp), and a nuclear marker, the internal transcribed spacers (ITS1 & ITS2; 1804 bp) from 49 stick insects. Mitochondrial DNA sequence divergences among the three genera (*Argosarchus*, *Clitarchus* and *Acanthoxyla*) were relatively high (similar to 12%) but the current taxonomy within genera was not supported. Within the three genera, low levels of genetic divergence were observed at both nuclear and mitochondrial loci, and phylogenetic analyses failed to support reciprocal monophyly of the two species in *Argosarchus* and *Clitarchus*. Sympatric individuals of *Argosarchus spiniger* and *A. horridus* were more closely related to each other than to members of their respective morphospecies from elsewhere. No males were found in the Chatham Island population of *Argosarchus* and although this population has been referred to as *A. schauinslandi*, genetic and morphological evidence does not support its distinction from mainland *Argosarchus*. Likewise, individuals identified as *Clitarchus tuberculatus* were genetically identical, or most similar to, *C. hookeri* from the same or adjacent sites rather than grouping with the stick insects they were morphologically most similar to. Lack of spatial, behavioural or ecological evidence concordant with the described species *A. spiniger*, *A. schauinslandi* and *C. tuberculatus* leads us to infer that these species are synonymies of *A. horridus* and *C. hookeri* respectively. We conclude that *Argosarchus* and *Clitarchus* have each been over-split and actually consist of a single morphologically polymorphic, facultative parthenogenetic species. The genus *Acanthoxyla* with eight described species also has low levels of genetic divergence, similar to those found in *Argosarchus* and *Clitarchus*. A possible hybrid origin of *Acanthoxyla* involving its sister genus *Clitarchus* is implied by sharing of ITS sequence variants, but further sampling is needed before the species status of these obligate parthenogenetic lineages can be resolved. In contrast to some New Zealand Orthoptera, the Phasmatinae show little genetic variation suggesting coalescence in recent times, possibly reflecting

lineage sorting in the Pleistocene.

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#### **Assortative preferences and discrimination by females against hybrid male song in the grasshoppers *Chorthippus brunneus* and *Chorthippus jacobsi* (Orthoptera : Acrididae)**

Bridle, JR; Saldamando, CI; Koning, W; Butlin, RK. 2006

The grasshoppers *Chorthippus brunneus* and *Chorthippus jacobsi* are highly differentiated for male mating signals, and form a mosaic hybrid zone in northern Spain. At some sites within this zone, many hybrids are observed. At others, few hybrids are observed. Such bimodal sites may reflect recent contacts between parental genotypes, or local variation in levels of assortative mating or selection against hybrids. Playback of 12 parental and F1 male songs to 296 parental and hybrid females revealed positive assortative preferences in *C. brunneus* and *C. jacobsi* females, supporting a direct role of male mating signals in female choice. However, all female genotypic classes showed reduced responsiveness to F1 male songs. Such sexual selection against hybrids is consistent with the narrow cline width observed in the field for song characters relative to morphology. These results have implications for the genetic structure of the hybrid zone and for models of speciation by reinforcement.

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#### **The characteristics of karyotype and telomeric satellite DNA sequences in the cricket, *Gryllus bimaculatus* (Orthoptera, Gryllidae)**

Yoshimura, A; Nakata, A; Mito, T; Noji, S. 2006

The chromosomes derived from the Japanese population of *Gryllus bimaculatus* were characterized by C-banding and Ag-NOR staining. The chromosome number,  $2n = 28 + XX$  (female)/ $XO$  (male), corresponded with that of other populations of *G. bimaculatus*, but the chromosome configuration in idiograms varied between the populations. NORs were carried on one pair of autosomes and appeared polymorphous. The positive C-bands located at the centromere of all chromosomes and the distal regions of many chromosome pairs, and the size and the distribution pattern of the distal C-heterochromatin showed differences among the chromosomes. In addition, this paper reports on the characteristics of HindIII satellite DNA isolated from the genome of *G. bimaculatus*. The HindIII repetitive fragments were about 0.54 kb long, and localized at the distal C-bands of the autosomes and the interstitial C-bands of the X chromosome. Molecular analysis showed two distinct satellite DNA sequences, named the GBH535 and GBH542 families, with high AT contents of about 67 and 66%, respectively. The two repetitive families seem to be derived from a common ancestral sequence, and both families possessed the same 13-bp palindrome sequence. The results of Southern blot hybridization suggest that the sequence of the GBH535 family is conserved in the genomic DNAs of *Gryllus* species, whereas the GBH542 family is a species-specific sequence.

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#### **Visual communication behaviour as a mechanism behind reproductive interference in three pygmy grasshoppers (Genus *Tetrix*, tetrigidae, orthoptera)**

Hochkirch, A; Deppermann, J; Groning, J. 2006

Specific mate recognition systems should enable species to recognize conspecific mates correctly. However, heterospecific matings have been observed in a variety of taxa. One of these cases is the pygmy grasshopper genus *Tetrix*, in which three species show sexual interactions. *T. ceperoi* males mount preferably females of *T. subulata*, but they are rejected as mates. *T. subulata* males prefer *T. undulata* females over conspecific females and heterospecific matings occur. Here, we study the underlying behavioural mechanisms of this pattern by analysing the visual courtship behaviour of the three species video-graphically. We test the hypothesis that the displays of *T. ceperoi* are highly differentiated from the other species, while the courtship of *T. subulata* and *T. undulata* is more similar. This is supported by our results: while *T. ceperoi* males perform a fast movement of high amplitude ("pronotal bobbing"), the other two species show only minor movements ("lateral swinging", "frontal swinging"). The first function of a discriminant analysis of the temporal dimensions of the displays explained 96% of the variance. 100% of the *T. ceperoi* displays were classified correctly, whereas only 50% of the *T. subulata* and 81% of the *T. undulata* displays were grouped accurately. A two-way ANOVA revealed no significant effects of the direction of the "swinging" movements (laterally or frontally) and no interactions between direction and species either, whereas each temporal parameter differed significantly between the three species. The highest degree of differentiation was found between *T. ceperoi* and *T. undulata*, while *T. subulata* and *T. undulata* only differed significantly in two of the six temporal parameters. Our results suggest that the mismatings between *T. undulata* and *T. subulata* are caused by an insufficient specificity of the courtship behaviour. Apparently, ecological segregation of these two species could impede sexual interactions in the field.

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#### **Gis-based niche models reveal unifying climatic mechanisms that maintain the location of avian hybrid zones in a North American suture zone**

Swenson, NG. 2006

The existence of suture zones in North America has recently been verified, yet the environmental factors responsible for the maintenance of their structure and position have remained undetermined. The Great Plains suture zone in the US is perhaps the most significant and broadly studied in North America. Numerous avian hybrid zones that cluster in this region have been extensively studied over the last half-century. A primary result of this work is that exogenous factors present in this region have promoted and maintained avian species divergence. Yet, to date the variables most important in the generation and the clustered positioning of these hybrid zones in relation to one another have not been determined. The present study aims to advance our understanding of this North American suture zone by using niche modelling to quantify which environmental variables are most important in its formation and maintenance. Through the generation of fundamental niches for four hybrids and their parental species, similarities linking the hybrid zones were uncovered. The results show that temperature holds this suture zone in position and also suggest that temperature played a primary role in promoting niche differentiation among these sister species pairs during Pleistocene glacial cycles.

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#### **A component of isolation between *Allonemobius shalontaki* (Orthoptera : Gryllidae : Nemobiinae) and a sympatric congener**

Birge, LM; Braswell, WE; Howard, DJ. 2007

*Allonemobius shalontaki* (Braswell) (Orthoptera: Gryllidae: Nemobiinae), a newly recognized species, was described on the basis of novel electrophoretic alleles and a unique male calling song. However, little is known about the species and the factors that isolate it from co-occurring species of *Allonemobius* (Hebard). We use electrophoretic markers to document sympatry of *A. shalontaki* with its congener *Allonemobius socius* (Scudder) and to follow the life cycle of the two species at two sites. The results indicate that there are phenological differences between the species. To confirm the phenological differences quantified in the field, we study patterns of egg development and hatching in the laboratory. Together with laboratory hybridization studies, these results demonstrate that *A. shalontaki* and *A. socius* are strongly, but not completely, reproductively isolated.

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#### **Hybridization between *Saga pedo* (Pallas 1771) and *Saga rammei* Kaltenbach 1965 (Orthoptera : Tettigoniidae)**

Lemonnier-Darcemont, M; Darcemont, C. 2007

Since 2004, hybridizations in captivity were tested between *Saga pedo* (Pallas 1771), a parthenogenetic species, and various bisexual closely related species of the Balkans *Saga hellenica* Kaltenbach 1967, *Saga rammei* Kaltenbach 1965 and *Saga campbelli* Uvarov 1921. Mating with formation of spermatophores were noted in all cases. The first hatching, resulting from a female of *S. pedo* with a male of *S. rammei*, occurred in April 2006.

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#### **Microsatellites in the striped ground crickets, *Allonemobius* (Orthoptera : Gryllidae)**

Birge, LM; Bogdanowicz, SM; Harrison, RG; Howard, DJ. 2007

Polymorphic di-, tri- and tetranucleotide repeats were examined in *Allonemobius* to determine whether they could serve as useful markers in studies of sperm precedence, population genetics and hybrid zone structure. Ten microsatellite DNA loci were sufficiently polymorphic to be used for paternity tests and showed no evidence of linkage disequilibrium or deviations from Hardy-Weinberg equilibrium in *Allonemobius socius*. Nine of 10 of these microsatellites can be amplified from three other *Allonemobius* species, suggesting that these markers will have widespread utility in this ground cricket genus.

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#### **The origin of the *Chorthippus parallelus* hybrid zone: chromosomal evidence of multiple refugia for Iberian populations**

Bella, JL; Serrano, L; Orellana, J; Mason, PL. 2007

A study of the variation in pattern and frequency of constitutive heterochromatin and nucleolar organizing regions of the X chromosomes of male *Chorthippus parallelus* grasshoppers in 25 populations within the Iberian peninsula requires us to revise our interpretation of the biogeography and evolutionary history of this species. Hybridization between the subspecies *Cp erythropus* and *Cp parallelus*, previously only known from populations in the Pyrenean cols, is shown to extend at least 400 km further into north-west Spain. A novel X-chromosome variant is described that appears to be close to fixation in 18 populations, mainly from the centre and south of Spain. Our findings indicate a possible independent origin for each of three distinct, nonderivative X variants present in Spain: the northern *Cp erythropus* and *Cp parallelus* variants, and a central-southern *Cp erythropus* variant. The first two are distinguished by interstitial and distal C bands, respectively, whereas the central-southern form has neither. This central-southern form is probably the current representative of the ancestral Iberian X variant. The pattern of variation supports the hypotheses of multiple refugia for Iberian populations and that more hybrid zones exist between these chromosomal variants.

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#### **Isolation mechanisms in the closely related grasshopper species, *Chorthippus albomarginatus* and *Ch. oschei* (Orthoptera, Acrididae)**

Vedenina, VY; Kulygina, NK; Panyutin, AK. 2007

Two closely related grasshopper species, *Chorthippus albomarginatus* and *Ch. oschei*, are known to hybridize at a narrow contact zone in the territory of Ukraine and Moldova. Different isolation mechanisms providing a reproductive isolation of these species were studied. In the mating experiments, females of both species demonstrated a strong assortative mating (80-90% preference for conspecific males). The comparison of the parental and hybrid viability revealed a reduced hatching and an increased larval mortality in F-1 and F-2 hybrids. In the choice mating experiments, the females mated less assortatively than parental females. The data obtained demonstrated the existence of pre- and post-mating isolation in *Ch. albomarginatus* and *Ch. oschei*. A possible fate of the hybrid zone is discussed.

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#### **The unusual inheritance pattern of the courtship songs in closely related grasshopper species of the *Chorthippus albomarginatus*-group (Orthoptera : Gomphocerinae)**

Vedenina, VY; Panyutin, AK; Von Helversen, O. 2007

Sibling species of the *Chorthippus albomarginatus*-group are exceptional among all European grasshopper species because they have an extremely elaborate courtship behaviour. Here, we present a genetic analysis of the courtship song differences between two closely related grasshopper species *Ch. albomarginatus* and *Ch. oschei*. Measurements of seven courtship song characters and one parameter of courtship visual display were compared among parentals, F-1 and F-2 hybrids, and backcrosses. Variation in one morphological character, the number of stridulatory pegs, was studied as well. The distributions of song phenotypes were more consistent with a type-III genetic architecture, which involves complementary or duplicate pairs of loci. We suggest that this type of architecture may provide the novel elements of the hybrid songs, even more complex than the parental ones, which may offer a new starting point for sexual selection. One parameter of the visual display appeared to be controlled by a single locus, but differences in other characters of visual display could be explained by a more complex inheritance pattern. Inheritance of the peg number differences was consistent with a simple polygenic additive model. Sex linkage and/or maternal effects were not detected for any trait. We found a disproportionate influence of the *Ch. albomarginatus* parent on most hybrid song characteristics and the visual display, and this may support a previously suggested idea that *Ch. albomarginatus* is an ancestral form and *Ch. oschei* is a derived species.

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#### **A discrete neuropeptide difference between two hybridizing grasshopper subspecies**

Roth, S; Kohler, G; Reinhardt, K; Predel, R. 2007

Population divergence can be detected by the divergence of functional and neutral characters. Under some circumstances, it is desirable to have available a character that is discretely expressed in either of the diverging genomes, rather than the evaluation of qualitative variation of continuous characters. In the present study, we investigated mass peaks of peptide hormones in a model system of population divergence, the hybrid zone of two *Chorthippus parallelus* subspecies in the French-Spanish Pyrenees. Mass spectra from neuroendocrine tissues have previously been identified as species-specific and may have a sufficient resolution to vary at the subspecies level. For the first time, we succeeded in the detection of a subspecies-specific expression of neuropeptides collected from single individuals. Mass spectra sampled from populations across the *C. parallelus* grasshopper hybrid zone indicated neuropeptide identity between the sexes and within sample sites. The distribution of a single distinct but variable peptide signal, however, very closely followed the cline of the hybrid zone as derived from the mean variation in several continuous characters. The identity of this peptide in populations from the northern Pyrenees and central Europe supports a neuropeptide differentiation of preglacial origin. The observed differentiation in the peptide profile of the two subspecies demonstrates that a peptidomic approach may be a promising perspective to reconstruct reproductive isolation in an insect hybrid zone. (C) 2007 The Linnean Society of London.

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#### **Description and biogeographical implications of a new species of the genus *Podisma* Berthold 1827 from Mont Ventoux in South France (Orthoptera : Acrididae)**

Fontana, P; Pozzebon, A. 2007

The status of the genus *Podisma* Berthold 1827 is discussed and all its taxa are listed. Endemic taxa within montane orthopteroid insects in southern Europe are considered and new genera recently revised are recorded. In this context *Podisma amedeignatoae* n. sp. from Mount Ventoux in the South Alps (France) is defined and described. The main distinctive characters of the new species are the relative length of prozona and metazona, the presence of the dotted dorsal pattern (FDDP) in almost 100% of the females, the broadly incised male furcula, the subquadrate dorsal valvae of the penis and the peculiar v-shaped middle incision diving them.

The presence of a distinct species on Mount Ventoux allows to suppose the presence of a refuge area in this region during the ice ages. The analysis of the distribution of the FDDP character, distributed from southern France to southeastern Italy, shows a clear interruption in the genetic flow between the western and eastern slopes (French and Italian slopes) in the western Alps. This interruption fits well with the presence of a hybrid zone, recorded in literature for the genus *Podisma* on the basis of the distribution in this area of two male sex-chromosome forms. On the other hand data concerning the distribution of FDDP suggest a genetic flow coming from Northwest to South-east. After that the description of *P. amedeagnatoe* is not only a new contribution to the knowledge of the biodiversity in the southern European mountains but adds new data to the study of the colonisation of Europe after the ice ages, by species which have survived in refuge areas.

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#### **Behavioral sterility of hybrid males in acoustically communicating grasshoppers (Acrididae, Gomphocerinae)**

Gottsberger, B; Mayer, F. 2007

The effectiveness of hybridization barriers determines whether two species remain reproductively isolated when their populations come into contact. We investigated acoustic mating signals and associated leg movements responsible for song creation of hybrids between the grasshopper species *Chorthippus biguttulus* and *C. brunneus* to study whether and how songs of male hybrids contribute to reproductive isolation between these sympatrically occurring species. Songs of F1, F2, and backcross hybrids were intermediate between those of both parental species in terms of phrase number and duration. In contrast, species-specific syllable structure within phrases was largely lost in hybrids and was produced, if at all, in an irregular and imperfect manner. These divergences in inheritance of different song parameters are likely the result of incompatibility of neuronal networks that control stridulatory leg movements in hybrids. It is highly probable that songs of hybrid males are unattractive to females of either parental species because they are intermediate in terms of phrase duration and lack a clear syllable structure. Males of various hybrid types (F1, F2, and backcrosses) are behaviorally sterile because their songs fail to attract mates.

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#### **Contrasting patterns of hybridization in large house spiders (Tegenaria atrica group, Agelenidae)**

Croucher, PJP; Jones, RM; Searle, JB; Oxford, GS. 2007

The integrity of species is not fixed and may vary geographically. Here we investigate the geographic distributions and interactions of species in the *Tegenaria atrica* group (Araneae: Agelenidae). Detailed mapping of *T. saeva* and *T. gigantea* in England and Wales shows them to be broadly allopatric in southern England with a tightly defined, and possibly long-standing, narrow zone of parapatry in central southern England. In the north of England (Yorkshire), by contrast, the species are broadly sympatric as a result of recent range expansions. GIS techniques are used to map the species distributions and to quantify, we believe for the first time, the intimacy of interspecific interactions. The extent and nature of hybridization in these two areas is examined through regression and multivariate analyses of morphology. We show that the relative incidence of hybridization is much greater in Yorkshire than within the parapatric zone in the south. Clear patterns of asymmetric introgression are observed in both northern and southern England, with a greater impact of *T. gigantea* on *T. saeva* than vice versa. We find no sign of morphological reproductive character displacement at the zone of parapatry that might indicate reinforcement, although we cannot exclude more subtle effects, for example via cuticular pheromones. The integrity of these two species seems to be breaking down in northern England, a process that might gain momentum as the gene pools become more similar.

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#### **Genetic differentiation of an endangered capercaillie (Tetrao urogallus) population at the Southern edge of the species range**

Rodriguez-Munoz, R; Mirol, PM; Segelbacher, G; Fernandez, A; Tregenza, T. 2007

The low-latitude limits of species ranges are thought to be particularly important as long-term stores of genetic diversity and hot spots for speciation. The Iberian Peninsula, one of the main glacial refugia in Europe, houses the southern distribution limits of a number of boreal species. The capercaillie is one such species with a range extending northwards to cover most of Europe from Iberia to Scandinavia and East to Siberia. The Cantabrian Range, in North Spain, constitutes the contemporary south-western distribution limit of the species. In contrast to all other populations, which live in pure or mixed coniferous forests, the Cantabrian population is unique in inhabiting pure deciduous forests. We have assessed the existence of genetic differentiation between this and other European populations using microsatellite and mitochondrial DNA (mtDNA) extracted from capercaillie feathers. Samples were collected between 2001 and 2004 across most of the current distribution of the Cantabrian population. Mitochondrial DNA analysis showed that the Cantabrian birds form a distinct clade with respect to all the other European populations analysed, including the Alps, Black Forest, Scandinavia and Russia, which are all members of a discrete clade. Microsatellite DNA from Cantabrian birds reveals the lowest genetic variation within the species in Europe. The existence of birds from both mtDNA clades in the Pyrenees and evidence from microsatellite frequencies for two different groups, points to the existence of a Pyrenean contact zone between European and Cantabrian type birds. The ecological and genetic differences of the Cantabrian capercaillies qualify them as an Evolutionarily Significant Unit and support the idea of the importance of the rear edge for speciation. Implications for capercaillie taxonomy and conservation are discussed.

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#### **Studies on the phylogeny of the genus Saga (Orthoptera: Tettigoniidae): chromosomal data.**

Lemonnier-Darcemont, M; Dutrillaux, AM; Dutrillaux, B; Darcemont, C. 2008

Combining the first cytogenetic analysis of four European *Saga* species, and the re-assessment of the karyotype of *Saga pedo* (Papas 1771), with published data and the results of investigations in the field, a phylogeny of the species included is proposed. The most ancestral karyotypes seem to be those of *Saga ornata* Burmeister 1839 and *Saga cappadocica* Werner 1903, with all autosomes being acrocentrics. The merge of two pairs of their chromosomes resulted in the karyotypes of *Saga natoliae* Serville 1839 and *Saga hellenica* Kaltenbach 1967, including one pair of large submetacentrics. These two karyotypes differ by a pericentric inversion on these large chromosomes, that probably took place in *S. natoliae*. *Saga campbelli* Uvarov 1921 and *Saga rammei* Kaltenbach 1965, got an additional chromosomal merge and therefore include two pairs of large submetacentrics. The karyotype of *S. rammei* has an additional distinctive feature in its heterochromatin. The karyotype of *S. pedo* is tetraploid, probably the result of juxtaposition of two diploid genomes as a result of hybridisation. The distinctive feature in heterochromatin of *S. rammei* is found on *S. pedo* into two distinct chromosomes. Although one could expect quadruplets or doublets of chromosomes, a wide diversity of single chromosomes was noted. This demonstrates that a high rate of chromosomal restructuring has modified the karyotype of *S. pedo*, after its transition to tetraploidy. These accumulated restructuring, resulting in a high heterozygosity, can be explained by the lack of meiotic barrier for this parthenogenetic species. During our recent research in the field in the south of Balkans, an area with a possible intergradation between *Saga pedo* and some bisexual closely related species was discovered. The chromosome analysis of specimens from this area will be a main subject for the continuation of our research.

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#### **Geographical patterns of chromosomal differentiation in the brachypterous grasshopper Podisma sapporensis (Orthoptera : Acrididae)**

Warchalowska-Sliwa, E; Tatsuta, H; Akimoto, SI; Maryanska-Nadachowska, A; Kowalczyk, M; Bugrov, A. 2008

The distribution patterns of the X0/XX and neo-XY/neo-XX chromosome races, subraces, and "hybrids" between subraces of the grasshopper *P. sapporensis* were analyzed. The origin of the observed variation is Robertsonian translocations between a sex chromosome and an autosome, and chromosome rearrangements. The fixation levels of inversions varied depending on geographic regions. No hybrid population is known implying that a strong reproductive isolation system exists in hybrids between the different chromosomal races. The probable reasons for the purity of X0 and neo-XY chromosome races and high chromosome polymorphism in

contact zones between chromosomal subraces are discussed. The presence of isolating barriers between chromosome races indicates a review of the taxonomic structure of *P. sapporensis* is required. It is proposed to divide *P. sapporensis* into two sibling species, which differ in the chromosome mechanisms of the sex determination system. The analysis of the distribution of chromosomal races and subraces of *P. sapporensis* allows a reconstruction of the history of this species in the Okhotsk sea region.

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#### **Arcyptera fusca and Arcyptera tornosi repetitive DNA families: whole-comparative genomic hybridization (W-CGH) as a novel approach to the study of satellite DNA libraries**

Pita, M; Zabal-Aguirre, M; Arroyo, F; Gosalvez, J; Lopez-Fernandez, C; De la Torre, J. 2008

Whole-comparative genomic hybridization (W-CGH) has been used to exemplify a simple methodology which allows identifying and mapping whole genome differences for highly repetitive DNA sequences between two related species of unknown genomic background. The use of this technique to the species binomy *Arcyptera fusca*/*Arcyptera tornosi* has allowed the identification of different DNA families mainly concentrated within the para-/peri-centromeric and distal heterochromatic regions of different chromosomes, which are differentially expanded in both genomes. Additionally, W-CGH allowed chromosome mapping of particular euchromatic regions immersed in the chromosome arms which have been affected by processes of DNA amplification and losses. A molecular approach was also conducted to analyse satellite DNA families in these species. We have found three different families showing an unequal representation in both species. Two of these families showed a centromeric location (EcoRV-390CEN and Sau3A-419CEN), whereas the last one was located at distal heterochromatic regions (Sau3A-197TEL). As *A. fusca* is a widely distributed species represented in most European high mountains, whereas *A. tornosi* is an endemic species represented in the Iberian Peninsula, the differences and resemblances reported here offer a good basis to support a close evolutionary relationship between both of the actually isolated species. Finally, W-CGH allowed identification of an asynchronic pattern of heterochromatin condensation through early prophase (characteristic in both species) which is uncommon or probably has been poorly analysed within classical early condensing chromosome domains through meiosis. The congruence of the obtained cytological and molecular results is analysed in light of the ancestral genome relationship between both species.

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#### **Experimental hybridization between X0 and XY chromosome races in the grasshopper *Podisma sapporensis* (Orthoptera : Acrididae). II. Cytological analysis of embryos and adults of F-1 and F-2 generations**

Warchalowska-Sliwa, E; Bugrov, AG; Sugano, Y; Maryaska-Nadachowska, A; Akimoto, S. 2008

Experimental hybridization of X0 and XY chromosome races of the brachypterous grasshopper *P. sapporensis* did not reveal pre-zygotic reproductive isolation. However, a partial zygotic barrier was found between the X0-standard race from Shimokawa and XY-standard chromosome race from Akan. Approximately 40% of embryos from females crossed with males from other chromosome races developed parthenogenetically, the remaining embryos were normal heterozygotes. Adult F<sub>1</sub> males and females from crosses of this type had properly developed testes and ovaries. Non-sister associations and other irregularities in meiosis were not observed in male meiosis. Crossing experiments demonstrated that hybrids between X0 and XY races occur to some extent. The absence of a hybrid zone between the X0 and XY chromosome races may be the result of selection against heterozygotes. Crosses between the XY-Tanno and X0-standard (Teine) subraces resulted in F-1 and F-2 generations in spite of the many chromosome differences between them such as a X-A translocation and fixed pericentric inversions in four pairs of autosomes. These results do not support the hypothesis that chromosomal differences play a key role in restricting gene flow between the X0 and XY races of *P. sapporensis*.

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#### **The past and future influence of geographic information systems on hybrid zone, phylogeographic and speciation research**

Swenson, NG. 2008

Over the past two decades geographers have developed an increasingly sophisticated technology termed a geographic information system (GIS). A GIS has the ability to store, map and analyse spatial data. The powerful analytical capabilities of a GIS could serve to enhance our understanding of the spatial component of the evolutionary process. In particular, phylogeographers, hybrid zone and speciation researchers could benefit enormously from incorporating this sophisticated technology from the discipline of geography, as they have done so readily from other disciplines (e.g. genetics). Indeed, an increasing number of researchers in these fields are beginning to include GIS analyses into their research programmes. Some of this integration has taken the form of analysing the spatial relationship between populations and hybrid zones. Several other researchers have also begun to incorporate GIS into their work through the use of GIS-based niche models. These models estimate a multidimensional niche for a species using known geo-referenced populations and digital climate maps. Here, I review the recent integration of GIS and GIS-based predictive niche models into the above evolutionary sub-disciplines. I also describe evolutionary analyses that could be further enhanced through the implementation of GIS.

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#### **The frequency of rDNA variants within individuals provides evidence of population history and gene flow across a grasshopper hybrid zone**

Keller, I; Veltsos, P; Nichols, RA. 2008

In the grasshopper *Podisma pedestris*, units of the ribosomal DNA (rDNA) multigene family are not identical, but comprise multiple genetic variants. We surveyed this variation using a novel pyrosequencing approach. The history of the study populations is well characterized as the pattern of colonization can be inferred from the distribution of two chromosomal races that invaded from different directions after the last glacial maximum and finally met to form a hybrid zone. This knowledge of the populations' ancestry allows us to draw inferences about the rate of change in rDNA composition. The rDNA data have, in turn, been revealing about the populations' ancestry, indicating a previously unsuspected route of postglacial colonization. The two chromosomal races were found to have genetically distinctive rDNA composition, demonstrating the persistence of differences for thousands of generations. It follows that the hybrid zone represents a natural experiment in which repeated crossing and backcrossing between these different rDNA lineages has occurred for over 8000 generations. The association between chromosomal race and rDNA composition has been broken down within the zone. It therefore appears that rDNA variants move freely across the zone and are not under opposing selection pressures in the two races, as had previously been suspected.

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#### **Apparent Hybridization Between *Trimerotropis agrestis* and *Trimerotropis maritima* (Orthoptera: Acrididae) in a Recently Disturbed Habitat**

Brust, ML; Hoback, WW; Wright, RJ. 2009

In Nebraska, the ranges of *Trimerotropis maritima* (eastern species) and *T. agrestis* (western species) overlap but populations usually remain separated by habitat preferences. The morphological and color differences between the species are described. However, around Lake McConaughy, a reservoir on the North Platte River which has declined markedly in depth as a result of recent drought, a habitat was created in which the two species coincide and hybridize frequently. The water level in this reservoir had dropped in excess of 20 meters as of 2007, resulting in large expanses of dunes grading into beach habitats. Grasshoppers were collected in the area from 2005 to 2007 and based on morphological characteristics appear to represent hybrids. Surveys of many other habitats in Nebraska produced no hybrids. This study indicates that the alteration of habitat by impoundment of a river followed by climatic change may have the potential to disrupt environmental boundaries that maintain the integrity of parapatric sibling species. As this habitat is the result of human landscape alterations, it suggests that our alterations have the potential to disrupt environmental characteristics that maintain the integrity of parapatric sibling species.



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## **THE CHORTHIPPUS ALBOMARGINATUS-GROUP (ORTHOPTERA: ACRIDIDAE: GOMPHOCERINAE) IN THE CARPATHIAN BASIN: TRACES OF HYBRIDIZATION BETWEEN C. ALBOMARGINATUS AND C. OSCHEI IN SOUTHERN SLOVAKIA**

Vedenina, V; Holusa, J; Kocarek, P. 2009

Specimens of the *Chorthippus albomarginatus*-group were studied from two localities near Ardovo in southern Slovakia. We analyzed the male Courtship songs and the stridulatory peg number on the inner side of the hind femora. During recording of courtship songs, the stridulatory movements of the hind legs were also recorded. On the basis of the courtship song analysis and the measurements of the peg number, the specimens from both populations are regarded as *C. oschei pusztaensis*. However, deviations in song and leg movements for some specimens are consistent with hybridization between *C. albomarginatus* and *C. oschei*. Our study provides evidence that *C. albomarginatus* and *C. oschei* hybridize in Slovakia.

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## **The Field Cricket *Gryllus assimilis* and Two New Sister Species (Orthoptera: Gryllidae)**

Weissman, DB; Walker, TJ; Gray, DA. 2009

In preparation for revisionary studies of western U.S. *Gryllus* field crickets, some eastern U.S. names for species with supposed transcontinental distributions must be resolved. One such species, *Gryllus assimilis* (F.), as currently characterized, occurs in the West Indies, Brazil, Central America, and Mexico, and in five of the southernmost U.S. states. Our studies of calling songs and morphology indicate that at least three species exist among these populations. The type locality of *G. assimilis* is Jamaica, but the type specimen is lost and two similar species of *Gryllus* occur there. One of these species occurs widely outside of Jamaica, and we assign it to *G. assimilis* and designate a neotype. The other occurs only in Jamaica and is assigned to *Gryllus jamaicensis* T. J. Walker n. sp. Nearly all populations formerly known as *G. assimilis* from southern California, southern Arizona, Southern Nevada, and Mexico west of the continental divide are assigned to *Gryllus multipulsator* Weissman n. sp. Populations located elsewhere (with one exception) are deemed conspecific with Jamaican *G. assimilis*, although *G. assimilis* from islands east and south of Hispaniola have calling songs with dominant frequencies higher than is characteristic of the species elsewhere. Studies of mitochondrial DNA of *assimilis*-type *Gryllus* from widespread localities are compatible with the above species classification. Hybridization trials between *G. assimilis* and *G. multipulsator* demonstrated high interfertility. *Gryllus contingens* F. Walker and *Gryllus mundus* F. Walker are removed from synonymy with *G. assimilis*.

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## **Molecular taxonomy and species delimitation in Andean *Schistocerca* (Orthoptera: Acrididae)**

Yassin, A; Amedegnato, C; Cruaud, C; Veuille, M. 2009

The acridian genus *Schistocerca* comprises about 50 species which are endemic to the New World, except the Old World locust *S. gregaria*. Their morphological identification is rendered difficult by phase polyphenism, geographical overlap due to migrations or swarming, the difficulty to easily differentiate genitalia and the occurrence of interspecific hybrids. The three species reported from Peru include the swarming species *S. interrita*, a pest that can be recognized only by taxonomists. We show that it can be unambiguously identified using a mitochondrial DNA fragment known to have barcoding properties in this genus. We used several methods to delimitate Peruvian species. While *S. interrita* and *S. pallens* were well characterized, *S. piceifrons peruviana* was split into several taxa by a phylogeny-based method, whereas a combination of population genetics methods led one to identify only the three nominal species. A tentative reconstruction of the species history shows that several populations of *S. piceifrons peruviana* have recently increased in number, while exchanging some migrants, whereas an isolated population at the northern margin of the species range is substantially differentiated while exchanging no migrants with the others. This complex history has resulted in an atypical lineage pattern that appears to have confounded the standard assumptions underlying available species delimitation methods. Because of its behavioral property which tends to keep it panmictic, the identification of the swarming *S. interrita* remained unaffected. (C) 2009 Elsevier Inc. All rights reserved.

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## **Peptides of the adipokinetic hormone/red pigment-concentrating hormone family with special emphasis on Caelifera: Primary sequences and functional considerations contrasting grasshoppers and locusts**

Gade, G; Marco, HG. 2009

The presented work is a hybrid of an overview and an original research paper. First, we review briefly the structure, biosynthesis, release, mode of action and function of those peptides that constitute the adipokinetic/red pigment-concentrating family. Second, we collate the data on primary sequences available for caeliferan orthoptera, i.e. grasshoppers and locusts, and add a number of new data from previously unpublished work data. The data are interpreted in conjunction with morphological and molecular biology with respect to phylogenetic relationships of these various taxa. Finally, we discuss the differences between the adipokinetic response of grasshoppers and locusts to corpus cardiacum extract or synthetic adipokinetic hormone with regard to flight ability, phase polymorphism, age, presence of adipokinetic hormones, lipophorin system and other parameters. It appears that the higher hyperlipaemic response is always correlated with pronounced flight ability. (C) 2008 Elsevier Inc. All rights reserved.

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## **Adaptation and selection in the *Senecio* (Asteraceae) hybrid zone on Mount Etna, Sicily**

Brennan, AC; Bridle, JR; Wang, AL; Hiscock, SJ; Abbott, RJ. 2009

P>Hybrid zone theory provides a powerful theoretical framework for measuring and testing gene flow and selection. The *Senecio aethnensis* and *Senecio chrysanthemifolius* hybrid zone on Mount Etna, Sicily, was investigated to identify phenotypic traits under divergent selection and to assess the contributions of intrinsic and extrinsic selection against hybrids to hybrid zone maintenance. *Senecio* samples from 14 sites across Mount Etna were analyzed for 24 quantitative traits classified into four groups (QTGs), six allozymes and seven simple sequence repeat (SSR) loci to describe patterns of variation throughout the hybrid zone. Narrower cline widths or shifts in cline centre position were observed for three QTGs relative to the molecular clines, indicating that these traits are likely to be under extrinsic environmental selection. Altitude was key to describing species distributions, but dispersal and intrinsic selection against hybrids explained patterns at smaller spatial scales. The hybrid zone was characterized by strong selection against hybrids, high dispersal rates, recent species contact and few loci differentiating QTGs based on indirect measures. These results support the hypothesis that extrinsic and intrinsic selection against hybrids maintains the hybrid zone and species distinctiveness despite gene flow between the two *Senecio* species on Mount Etna. *New Phytologist* (2009) 183: 702-717doi: 10.1111/j.1469-8137.2009.02944.x.

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## **Multiple barriers to gene exchange in a field cricket hybrid zone**

Maroja, LS; Andres, JA; Walters, JR; Harrison, RG. 2009

Data on patterns of variation within hybrid zones, combined with studies of life history, mate choice, and hybrid performance, allow estimates of the contribution of different pre-zygotic and post-zygotic barriers to reproductive isolation. We examine the role of behavioural barriers to gene exchange in the maintenance of a hybrid zone between North American field crickets *Gryllus firmus* and *Gryllus pennsylvanicus*. We consider these barriers in the context of previous studies that documented



temporal and ecological isolation and a one-way post-mating incompatibility (i.e. *G. firmus* females do not produce offspring when they mate only with heterospecific males). Based on no-choice mating experiments in the laboratory, we demonstrate strong behavioural pre-mating barriers between the two species, but no apparent fecundity or fertility costs for *G. firmus* females when they mate with both conspecific and heterospecific males. Furthermore, we show that *G. firmus* females do not discriminate between hybrids and conspecifics, whereas *G. pennsylvanicus* females do. This observation could explain the asymmetric allele introgression observed in the hybrid zone. We also document a failure of heterospecific males to induce normal oviposition in *G. firmus* females, which may be due to rapid evolution of accessory gland proteins and may serve as an additional barrier to gene exchange. (C) 2009 The Linnean Society of London, Biological Journal of the Linnean Society, 2009, 97, 390-402.

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#### **Embryonic diapause highlighted by differential expression of mRNAs for ecdysteroidogenesis, transcription and lipid sparing in the cricket *Allonemobius socius***

Reynolds, JA; Hand, SC. 2009

Embryos of the ground cricket, *Allonemobius socius*, enter diapause 4-5 days post-oviposition and overwinter in this dormant state that is characterized by developmental arrest. Suppressive subtractive hybridization and quantitative real-time PCR reveal eight candidate genes in pre-diapause embryos that show promise as regulators of diapause entry, when compared with embryos not destined for diapause. Identifications are based both on the magnitude/consistency of differential mRNA abundances and the predicted functions of their products when placed in context of the physiological and biochemical events of diapause characterized in our companion paper. The proteins CYP450, AKR and RACK1 (associated with ecdysteroid synthesis and signaling) are consistently upregulated in pre-diapause, followed by major downregulation later in diapause. The pattern suggests that elevated ecdysone may facilitate onset of diapause in *A. socius*. Upregulation seen for the transcription factors Reptin and TFDp2 may serve to depress transcription and cell cycle progression. Cathpesin B-like protease, ACLY and MSP are three downregulated genes associated with yolk mobilization and/or metabolism that we predict may promote lipid sparing. Finally, embryos that have been in diapause for 10 days show a substantially different pattern of mRNA expression compared with either pre-diapause or embryos not destined for diapause, with the majority of mRNAs examined being downregulated. These transcript levels in later diapause suggest that a number of upregulated genes in pre-diapause are transiently expressed and are less essential as diapause progresses.

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#### **The ecology and agronomy of *Miscanthus sinensis*, a species important to bioenergy crop development, in its native range in Japan: a review**

Stewart, JR; Toma, Y; Fernandez, FG; Nishiwaki, A; Yamada, T; Bollero, G. 2009

Among several candidate perennial taxa, *Miscanthus x giganteus* has been evaluated and promoted as a promising bioenergy crop. Owing to several limitations, however, of the sterile hybrid, both at the taxon and agronomic production levels, other options need to be explored to not only improve *M. x giganteus*, which was originally collected in Japan, but to also consider the development of other members of its genus, including *Miscanthus sinensis*, as bioenergy crops. Indeed, there is likely much to be learned and applied to *Miscanthus* as a bioenergy crop from the long history of intensive interaction between humans and *M. sinensis* in Japan, which in some regions of the country spans several thousand years. Combined with its high amount of genetic variation, stress tolerance, biotic interactions with fauna, and function as a keystone species in diverse grasslands and other ecosystems within its native range, the unique and extensive management of *M. sinensis* in Japan as a forage grass and building material provides agronomists, agroecologists, and plant breeders with the capability of better understanding this species in terms of potential contribution to bioenergy crop development. Moreover, the studies described in this review may serve as a platform for future research of *Miscanthus* as a bioenergy crop in other parts of the world.

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#### **Variation in the Shape of Genital Appendages Along a Transect Through Sympatric and Allopatric Areas of Two Brachypterous Grasshoppers, *Parapodisma setouchiensis* and *Parapodisma subastris* (Orthoptera: Podisminae)**

Kawakami, Y; Tatsuta, H. 2010

Divergence in genital traits between closely related species is occasionally greater in sympatry than in allopatry, possibly because directional selection facilitates differentiation so as to prevent unfit hybridization. Here, we report for the first time that the shape of a functional genital structure, cercus, differs markedly between sympatrically and allopatrically occurring individuals in two brachypterous grasshopper species, *Parapodisma setouchiensis* Inoue 1979 and *Parapodisma subastris* Huang 1983 (Orthoptera: Podisminae). Although in areas of allopatry the cerci were straight in both species, in areas of sympatry the cerci of *P. setouchiensis* had an almost orthogonal bend. Furthermore, the angles of curvature of the cerci of *P. setouchiensis* varied continuously along a transect through sympatric and allopatric areas. We also observed copulation behavior in pairs and found that the apical part of the cerci was inserted into the space between the posterior edges of the seventh abdominal sternite and the seventh abdominal tergite of the female. We suggest that the orthogonally bent cerci allows the male to obtain a firm grip on the female's abdomen and propose that the conspicuous variation in the cerci of *P. setouchiensis* contributes to the strength of reinforcement of a premating isolation system.

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#### **Relative effects of juvenile and adult environmental factors on mate attraction and recognition in the cricket, *Allonemobius socius***

Olvido, AE; Fernandes, PR; Mousseau, TA. 2010

Finding a mate is a fundamental aspect of sexual reproduction. To this end, specific-mate recognition systems (SMRS) have evolved that facilitate copulation between producers of the mating signal and their opposite-sex responders. Environmental variation, however, may compromise the efficiency with which SMRS operate. In this study, the degree to which seasonal climate experienced during juvenile and adult life-cycle stages affects the SMRS of a cricket, *Allonemobius socius* (Scudder) (Orthoptera: Gryllidae) was assessed. Results from two-choice behavioral trials suggest that adult ambient temperature, along with population and family origins, mediate variation in male mating call, and to a lesser extent directional response of females for those calls. Restricted maximum-likelihood estimates of heritability for male mating call components and for female response to mating call appeared statistically nonsignificant. However, appreciable "maternal genetic effects" suggest that maternal egg provisioning and other indirect maternal determinants of the embryonic environment significantly contributed to variation in male mating call and female response to mating calls. Thus, environmental factors can generate substantial variation in *A. socius* mating call, and, more importantly, their marginal effect on female responses to either fast-chirp or long-chirp mating calls suggest negative fitness consequences to males producing alternative types of calls. Future studies of sexual selection and SMRS evolution, particularly those focused on hybrid zone dynamics, should take explicit account of the loose concordance between signal producers and responders suggested by the current findings.

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#### **Distribution of *Wolbachia* infection in *Chorthippus parallelus* populations within and beyond a Pyrenean hybrid zone**

Zabal-Aguirre, M; Arroyo, F; Bella, JL. 2010

Two subspecies of the meadow grasshopper *Chorthippus parallelus* meet in a secondary hybrid zone in the Pyrenees. We have recently detected *Wolbachia* infection in this extensively studied species. *C. p. parallelus* (Cp) and *C. p. erythropus* (Cpe) harbour bacteria from the B and F supergroups, but they differ noticeably in the incidence and type of infection present in their populations. We can distinguish different regional infection patterns that are associated with the distribution of pure and hybrid *C. parallelus* individuals. The northern pattern of low-level infection characterizes Cp populations, whereas the southern pattern of high-level infection

affects Cpe locations. These patterns converge in the hybrid zone and generate a third infection pattern featuring an extremely high degree of co-infection with the two *Wolbachia* types in hybrids. The distribution of *Wolbachia* among the studied populations encourages us to consider the possibility that this bacterium has a significant influence on the origin, maintenance and dynamics of this hybrid zone, given the reproductive alterations that are often associated with *Wolbachia*. *Heredity* (2010) 104, 174-184; doi:10.1038/hdy.2009.106; published online 9 September 2009

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## ASSORTATIVE MATING AND SPATIAL STRUCTURE IN HYBRID ZONES

M'Gonigle, LK; FitzJohn, RG. 2010

The spatial genetic composition of hybrid zones exhibits a range of possible patterns, with many characterized by patchy distributions. While several hypothetical explanations exist for the maintenance of these "mosaic" hybrid zones, they remain virtually unexplored theoretically. Using computer simulations we investigate the roles of dispersal and assortative mating in the formation and persistence of hybrid zone structure. To quantify mosaic structure we develop a likelihood method, which we apply to simulation and empirical data. We find that long distance dispersal can lead to a patchy distribution that assortative mating can then reinforce, ultimately producing a mosaic capable of persisting over evolutionarily significant periods of time. By reducing the mating success of rare males, assortative mating creates a positive within-patch frequency-dependent selective pressure. Selection against heterozygotes can similarly create a rare-type disadvantage and we show that it can also preserve structure. We find that mosaic structure is maintained across a range of assumptions regarding the form and strength of assortative mating. Interestingly, we find that higher levels of mosaic structure are sometimes observed for intermediate assortment strengths. The high incidence of assortment documented in hybrid zones suggests that it may play a key role in stabilizing their form and structure.

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## B chromosome ancestry revealed by histone genes in the migratory locust

Teruel, M; Cabrero, J; Perfectti, F; Camacho, JPM. 2010

In addition to the standard set of chromosomes (A), about 15% of eukaryote genomes carry B chromosomes. In most cases, B chromosomes behave as genomic parasites being detrimental for the individuals carrying them and prospering in natural populations because of transmission advantages (drive). B chromosomes are mostly made up of repetitive DNA sequences, especially ribosomal DNA (rDNA), satellite DNA and mobile elements. In only two cases have B chromosomes been shown to carry protein-coding genes. Although some B chromosomes seem to have derived from interspecific hybridisation, the most likely source of B chromosomes is the host genome itself, but the specific A chromosome being the B ancestor has not been identified in any B-containing species. Here, we provide strong evidence for B chromosome ancestry in the migratory locust, based on the location of genes for the H3 and H4 histones in the B chromosome and a single A chromosome pair (i.e. the eighth in order of decreasing size). The high DNA sequence similarity of A and B chromosome H3-H4 genes supports B-origin from chromosome 8. The higher variation shown by B sequences, compared to A sequences, suggests that B chromosome sequences are most likely inactive and thus less subjected to purifying selection. Estimates of time of divergence for histone genes from A and B chromosomes suggest that B chromosomes are quite old (> 750,000 years), showing the B-chromosome ability to persist in natural populations for long periods of time.

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## Hybridation between *Saga campbelli* Kaltenbach 1965 and *Saga hellenica* Kaltenbach 1967 (Orthoptera: Tettigoniidae).

Lemonnier-Darcemont, M; Dutrillaux, AM; Dutrillaux, B; Darcemont, C. 2011

Hybridation between *Saga campbelli* Kaltenbach 1965 and *Saga hellenica* Kaltenbach 1967 (Orthoptera: Tettigoniidae). Within the scope of its current studies on *Saga* genus, the G.E.E.M. has noted in May 2009 the hatching from breeding of one male and one female, issued from breeding, from a cross-mating between a *Saga campbelli* Kaltenbach 1965 female and a *Saga hellenica* Kaltenbach 1967 male. The cytogenetic study of the hybrid female confirms its hybrid origin and that only one Robertsonian translocation separates the karyotypes of *S. hellenica* and *S. campbelli*. The appearance of the male seems to be closer to *S. hellenica* than *S. campbelli*.

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## Asymmetric mate choice, hybridization, and hybrid fitness in two sympatric grasshopper species

Hochkirch, A; Lemke, I. 2011

Hybridization between animal species has long been regarded as unusual, but is meanwhile accepted as a widespread phenomenon. Typically, sexual interactions among species are studied in secondary contact zones of closely related species (hybrid zones) or between invasive and native species, whereas hybridization between sympatric congeners has received little attention. Here, we present a study on the hybridization potential of two grasshopper species, *Chorthippus parallelus* and *Chorthippus montanus*, which occur sympatric in large parts of Eurasia. We performed a mate choice experiment with specimens from an area of local parapatry in northwestern Germany. Most copulations were conspecific, but males of both species and females of *C. parallelus* were indiscriminate in their mate choice, while females of *C. montanus* clearly preferred conspecific males. Although these results suggest asymmetric introgression, a no-choice hybridization experiment revealed that hybridization is possible in both directions. The hatching success of the hybrids was intermediate between the parental species. Female hybrids showed no clear mate preferences, indicating that back crossing in both directions is possible in principle, but the fertility of the hybrids and the fitness of the F2 generation remain unknown. Our study suggests that hybridization between sympatric species might occur more often than assumed. It might affect the ecology and local distribution of animals in a similar way as competition does.

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## THE DIFFERENTIAL GRASSHOPPER (ORTHOPTERA: ACRIDIDAE)-ITS IMPACT ON TURFGRASS AND LANDSCAPE PLANTS IN URBAN ENVIRONS

Reinert, JA; Mackay, W; Engelke, MC; George, SW. 2011

The differential grasshopper, *Melanoplus differentialis* (Thomas) (Orthoptera: Acrididae), frequently migrates from highway rights-of-way, pastures, and harvested fields to feed in urban/suburban landscapes and retail/wholesale nurseries across the southern and southwestern U.S.A., as these areas dry down during hot dry summers. Nine selected turfgrasses and 15 species of landscape plants were evaluated for their susceptibility or resistance to this grasshopper. Grasshoppers were collected from stands of Johnsongrass, *Sorghum halepense*, which was used as a standard host for comparison in both experiments. Based on feeding damage, number of grasshopper fecal pellets produced, and their dry weight, *Zoysia matrella* cv. 'Cavalier' was the least preferred grass followed by *Buchloe dactyloides* cv. 'Prairie' and *Z. japonica* cv. 'Meyer'. *Festuca arundinacea* was significantly the most preferred host and sustained the most feeding damage, followed by *Poa pratensis* x *P. arachnifera* cv. 'Reveille' and 2 *Cynodon* spp. cultivars, 'Tifway' and 'Common'. Among the landscape plants, *Hibiscus moscheutos* cv. 'Flare', *Petunia violacea* cv. 'VIP', *Phlox paniculata* cv. 'John Fanick', *Tecoma stans* cv. 'Gold Star', and *Campsis grandiflora* were the least damaged or most resistant. *Plumbago auriculata* cv. 'Hullabaloo', *Glandularia* hybrid cv. 'Blue Princess', *Canna x generalis*, Johnsongrass, and *Cortaderia selloana* cv. 'Pumila' sustained the most damage. Based on the number of fecal pellets produced and their weights, *Canna x generalis* and *Glandularia* hybrid cv. 'Blue Princess' were the most preferred landscape plants tested.

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## **Reproductive Isolation Between Two Populations of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) Collected in Corn and Rice Fields From Central Colombia**

Velasquez-Velez, MI; Saldamando-Benjumea, CI; Rios-Diez, JD. 2011

*Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) is a Neotropical moth that has diverged into corn, *Zea mays* L., and rice, *Oryza sativa* L., host strains because these plants are their most frequently used hosts. The corn strain also has been found in cotton, *Gossypium hirsutum* L., and sorghum, *Sorghum bicolor* (L.) Moench, and the rice strain in small grasses and pasture grasses. Studies of the reproductive isolation between these two strains have provided ambiguous results from populations in the United States. In Colombia, we tested pre- and postzygotic isolation in these strains. Both strains showed postzygotic isolation for several life-history traits, including number of egg masses, number of larvae, number of females, pupal developmental time, female and male longevity, and female and male pupal weight. We observed a reduction of the number of hybrid females and a reduction in fertility in hybrids in *S. frugiperda*. These results suggest the possibility of Haldane's rule. Heterosis in the F<sub>1</sub>(2) and F<sub>2</sub>(1) generations was observed for number of larvae and adult longevity. This line presented a high standard deviation, suggesting instability in this cross. A possible effect of the X chromosome may explain the reduction in viability and sterility in F<sub>1</sub> hybrids of host strains of *S. frugiperda*. No temporal isolation was observed between the corn and rice strains. Differences in longevity between corn and rice strains might be another form of temporal isolation between these strains, because differences in adulthood time might reduce the encounters between them and thus hybridization.

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## **Variation in complex courtship traits across a hybrid zone between grasshopper species of the *Chorthippus albomarginatus* group**

Vedenina, V. 2011

Closely related grasshopper species of the *Chorthippus albomarginatus* group are notable for their extremely complex courtship songs, accompanied by a visual display. Two species of this group, *Ch. albomarginatus* and *Ch. oschei*, were previously shown to hybridize in a wide mosaic hybrid zone in Ukraine and Moldova. In this paper, variation in five courtship song characters, one character of visual display and the number of stridulatory pegs were analysed across the hybrid zone to estimate selection against hybrids and strength of assortative mating. Comparison of cline width and position across the hybrid zone showed concordant and coincident clines in four traits, such as three song characters and one morphological character, and discordant and non-coincident clines in two other song characters and the character of visual display. Concordance of clines in different characters suggests an equal strength of selection acting on underlying loci. Increase of variance and covariance between phenotypic traits at the cline centre could more likely result from assortative mating than from selection against hybrids. Most pairwise cases showed the highest covariance for the *oschei*-like, than for the *albomarginatus*-like hybrid populations. This indicates that introgression of the *oschei* genes into the *albomarginatus* genome is stronger than vice versa, and may be evidence of the movement of the hybrid zone in favour of *Ch. albomarginatus*. Analysis of associations between phenotype and local vegetation showed that mosaic structure of the hybrid zone is explained to a great extent by habitat-phenotype associations. (C) 2011 The Linnean Society of London, Biological Journal of the Linnean Society, 2011, 102, 275-291.

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## **Morphological, Genetic, and Chromosomal Variation at a Small Spatial Scale within a Mosaic Hybrid Zone of the Grasshopper *Dichroplus pratensis* Bruner (Acrididae)**

Mino, CI; Gardenal, CN; Bidau, CJ. 2011

Hybrid zones are regions where genetically different populations meet and mate, resulting in offspring of mixed characteristics. In organisms with limited dispersal, such as melanopline grasshoppers, hybrid zones can occur at small spatial scales (i.e., < 500 m). We assessed levels of morphological, chromosomal, and molecular variability in adult males of the grasshopper *Dichroplus pratensis* Bruner (N = 137 males, 188 females) collected at 12 sites within a mosaic hybrid zone in a heterogeneous environment in Sierra de la Ventana, Argentina. In this hybrid zone, 2 Robertsonian chromosomal races, polymorphic for different centric fusions, meet (the "Northern race" at low altitudes and the "Southern race" at higher altitudes), forming hybrids that show monobrachial homologies during meiosis. High morphometric variation in 6 traits was revealed among grasshoppers of both sexes, with male body size positively and significantly correlated with increasing altitude. Frequency of Robertsonian fusions characteristic of the Southern race increased significantly with altitude. Moreover, fusion frequencies covaried between samples. Considerable genetic variation was revealed by random amplification of polymorphic DNA markers, with heterozygosity ranging from 0.3477 to 0.3745. Insects from low-altitude and high-altitude populations showed significant genetic differentiation, as indicated by F-ST values. The proposed model for *D. pratensis*, involving the generation and maintenance by chromosomal fusions, of gene complexes adaptive in different environments, could explain the observed clinal patterns within the contact zone.

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## **Habitat Association and Seasonality in a Mosaic and Bimodal Hybrid Zone between *Chorthippus brunneus* and *C. jacobsi* (Orthoptera: Acrididae)**

Bailey, RI; Saldamando-Benjumea, CI; Tatsuta, H; Butlin, RK. 2012

Understanding why some hybrid zones are bimodal and others unimodal can aid in identifying barriers to gene exchange following secondary contact. The hybrid zone between the grasshoppers *Chorthippus brunneus* and *C. jacobsi* contains a mix of allopatric parental populations and inter-mingled bimodal and unimodal sympatric populations, and provides an ideal system to examine the roles of local selection and gene flow between populations in maintaining bimodality. However, it is first necessary to confirm, over a larger spatial scale, previously identified associations between population composition and season and habitat. Here we use cline-fitting of one morphological and one song trait along two valley transects, and intervening mountains, to confirm previously identified habitat associations (mountain versus valley) and seasonal changes in population composition. As expected from previous findings of studies on a smaller spatial scale, *C. jacobsi* dominated mountain habitats and mixed populations dominated valleys, and *C. brunneus* became more prevalent in August. Controlling for habitat and incorporating into the analysis seasonal changes in cline parameters and the standard errors of parental trait values revealed wider clines than previous studies (best estimates of 6.4 to 24.5 km in our study versus 2.8 to 4.7 km in previous studies) and increased percentage of trait variance explained (52.7% and 61.5% for transects 1 and 2 respectively, versus 17.6%). Revealing such strong and consistent patterns within a complex hybrid zone will allow more focused examination of the causes of variation in bimodality in mixed populations, in particular the roles of local selection versus habitat heterogeneity and gene flow between differentiated populations.

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## **Potential Negative Effects of Earthworm Prey on Damage to Turfgrass by Omnivorous Mole Crickets (Orthoptera: Gryllotalpidae)**

Xu, Y; Held, DW; Hu, XP. 2012

The severity of damage to host plants by omnivorous pests can vary according to the availability of plant and animal prey. Two omnivorous mole crickets, *Scapteriscus vicinus* Scudder and *S. borellii* Giglio-Tos, were used to determine if the availability of prey influences damage to hybrid bermudagrass by adult mole crickets. Experiments were conducted in arenas with either grass alone (control), grass plus one mole cricket, grass plus earthworms (*Eisenia fetida* Savigny), or grass with earthworms and a mole cricket. Root growth variables (e.g., volume, dry weight) after 4wk and weekly measurements of top growth were compared among the treatments. Surprisingly, bermudagrass infested with either mole cricket species caused no significant reduction in root growth and a minimal reduction on top growth with *S. vicinus* compared with controls. Survival of earthworms with *S. borellii* was significantly lower than survival in the earthworm-only treatment suggesting predation. Survival of earthworms with *S. vicinus*, however, was not different from the earthworm-only treatment. The addition of earthworm prey with mole crickets did not significantly impact bermudagrass root or shoot growth relative to grass with only mole crickets. Despite no negative impacts from earthworms or mole crickets separately, earthworms plus mole crickets negatively impact several root parameters (e.g., length) suggesting an interaction between these two soil-dwelling invertebrates. Increased use of more target-selective insecticides in turfgrass may increase available prey. This work suggests that alternative prey, when present, may result in a negative impact on turfgrass roots from foraging omnivorous mole crickets.

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## A Genome Scan and Linkage Disequilibrium Analysis among Chromosomal Races of the Australian Grasshopper *Vandiemena viatica*

Jackson, B; Kawakami, T; Cooper, S; Galindo, J; Butlin, R. 2012

In the past decade the interest surrounding the role of recombination in speciation has been re-kindled by a new generation of chromosomal speciation models that invoke the recombination-suppression properties of some types of chromosomal rearrangement. A common prediction of recombination-suppression models is that gene exchange between diverging populations will be more restricted in regions of the genome that experience low recombination. We carried out a genome scan of three chromosomal races of the grasshopper *Vandiemena viatica* (Orthoptera: Morabinae), occurring on Kangaroo Island, South Australia, using 1517 AFLP loci, with a view to elucidating the roles that selection and chromosomal variation have played in the formation of these taxa. An analysis of molecular variance demonstrated that chromosomal race accounted for a significant proportion of the genetic variance in the total dataset, which concurred with the findings of an earlier study. Sampling across one previously-identified hybrid zone, and the identification of outlier loci between parental races allowed us to establish that, in admixed populations, outlier loci which potentially pre-date the isolation of populations of races on Kangaroo Island exhibit higher levels of linkage disequilibrium with each other than putatively neutral loci. In turn this suggests that they might reside within genomic regions of low recombination, or be closely linked with each other.

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## A narrow hybrid zone between the grasshoppers *Stenobothrus clavatus* and *Stenobothrus rubicundus*: courtship song analysis

Vedenina, V; Sradnick, J; Klopfel, A; Elsner, N. 2012

The closely related grasshopper species *Stenobothrus rubicundus* and *Stenobothrus clavatus* are known to hybridize in a very narrow contact zone on Mt. Tomaros in northern Greece. These species produce very different and complex courtship songs accompanied with visual display. We analyzed the courtship songs and underlying stridulatory movements of the hind legs in natural hybrids from Mount Tomaros. The two species were also hybridized in the laboratory and their songs were compared with the songs of the natural hybrids. Some hybrid songs were shown to have intermediate features between parental songs, whereas other hybrid songs comprised completely new elements. The *clavatus*-like song elements were found to dominate in hybrid songs. These song features may influence the mating success of hybrid males in the contact zone. A comparison of hybrid songs with the song pattern of the north European *S. rubicundus* populations allowed us to suggest a scenario of *S. rubicundus* and *S. clavatus* origin. (c) 2012 The Linnean Society of London, Biological Journal of the Linnean Society, 2012, .

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## Parental phase status affects the cold hardiness of progeny eggs in locusts

Wang, HS; Ma, ZY; Cui, F; Wang, XH; Guo, W; Lin, Z; Yang, PC; Kang, L. 2012

1. The capacity to adapt to low temperature is critical for the persistence of insect populations in heterogeneous environments. Locusts show remarkable phenotypic plasticity, termed phase change, in response to local population density. 2. In this study, the hypothesis that population density, as a social factor, affects the cold hardiness of progeny is validated in the migratory locust, *Locusta migratoria*, which shows remarkable density-dependent phase changes between gregarious and solitary phases. 3. We demonstrated that eggs of gregarious and solitary migratory locusts significantly differ not only in size and weight, but also in cold hardiness. Eggs of solitary locusts are more resistant to cold stress compared with those of gregarious locusts, with longer 50% lethal time at different low temperatures and under different acclimation treatments of cooling rates or cold exposure time, lower upper limit of chill injury zone, and lower sum of injurious temperature resulting from temperature-time regression. The lowest cooling rate (0.05 degrees C min<sup>-1</sup>) yields the highest survival of cold for eggs. 4. A custom-made microarray covering 9154 unigenes of the migratory locust demonstrated quite different gene expression profiles in the two phases in response to normal or low temperature. Under cold stress, the gregarious-phase eggs have higher transcriptional levels of heatshock proteins, DOPA decarboxylases and tyrosine hydroxylase, whereas the solitary-phase eggs exhibit stimulated lipid metabolism and carboxylic acid transport. 5. Hybridization between the two phases showed that the cold hardiness of eggs from the hybrid with solitary females is significantly higher than that of the hybrid with gregarious females, and the cold hardiness of eggs from each reciprocal hybrid is close to their maternal origins. These results indicate that the cold hardiness of progeny is affected by the parental phase status.

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## Comparative Genetic Structure and Demographic History in Endemic Galapagos Weevils

Sequeira, AS; Stepien, CC; Sijapati, M; Albelo, LR. 2012

The challenge of maintaining genetic diversity within populations can be exacerbated for island endemics if they display population dynamics and behavioral attributes that expose them to genetic drift without the benefits of gene flow. We assess patterns of the genetic structure and demographic history in 27 populations of 9 species of flightless endemic Galapagos weevils from 9 of the islands and 1 winged introduced close relative. Analysis of mitochondrial DNA reveals a significant population structure and moderately variable, though demographically stable, populations for lowland endemics ( $F_{ST} = 0.094-0.541$ ;  $\pi: 0.014-0.042$ ; Mismatch  $P = 0.003-0.026$ ; and  $D-(Tajima) = 0.601$  to  $1.203$ ), in contrast to signals of past contractions and expansions in highland specialists on 2 islands (Mismatch  $P = 0.003-0.026$  and  $D-(Tajima) = -0.601$  to  $1.203$ ). We interpret this series of variable and highly structured population groups as a system of long-established, independently founded island units, where structuring could be a signal of microallopatric differentiation due to patchy host plant distribution and poor dispersal abilities. We suggest that the severe reduction and subsequent increase of a suitably moist habitat that accompanied past climatic variation could have contributed to the observed population fluctuations in highland specialists. We propose the future exploration of hybridization between the introduced and highland endemic species on Santa Cruz, especially given the expansion of the introduced species into the highlands, the sensitivity to past climatic variation detected in highland populations, and the potentially threatened state of single-island endemics.

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## Wolbachia Induced Cytogenetical Effects as Evidenced in *Chorthippus parallelus* (Orthoptera)

Sarasa, J; Bernal, A; Fernandez-Calvin, B; Bella, JL. 2013

The cytoplasmic incompatibility induced by the bacterial endosymbiont *Wolbachia* is attributed to chromatin modification in the sperm of infected individuals and is only 'rescued' by infected females after fertilization. *Chorthippus parallelus* is a grasshopper with 2 subspecies that form a hybrid zone in the Pyrenees in which this *Wolbachia* - generated cytoplasmic incompatibility has recently been described. The analysis of certain cytogenetic traits (sex chromosome-linked heterochromatic bands, nucleolar organizing region expression, spermatid size and morphology, and number of chiasmata formed) in pure and hybrid *Chorthippus parallelus* that are infected and not infected by this bacterium indicates that the infection affects some of these traits and, in the case of the spermatids, reveals a synergism between the infection and the hybrid condition. These results are interpreted as being secondary effects of the chromatin modification induced by *Wolbachia* which thereby support this model of modification/rescue. The possible effects of these cytogenetic variations on affected individuals are also considered. Copyright (C) 2012 S. Karger AG, Basel

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## A narrow hybrid zone between the grasshoppers *Stenobothrus clavatus* and *Stenobothrus rubicundus* (Orthoptera: Gomphocerinae): female preferences for courtship songs

Vedenina, V; Fahsing, S; Sradnick, J; Klopfel, A; Elsner, N. 2013

Two grasshopper species, *Stenobothrus rubicundus* and *Stenobothrus clavatus*, were previously shown to hybridize in a narrow contact zone on Mount Tomaros in northern Greece. The species are characterized by complex and completely different courtship songs. In the present study, we investigated female preferences for the courtship songs of *S. rubicundus*, *S. clavatus* and hybrids in playback experiments. Playback of the courtship songs revealed assortative preferences in females of the parental species: they significantly more often preferred the songs of conspecific males. Hybrid females showed a lower selectivity than parental females, responding somewhat equally eager to playback of the songs of *S. clavatus*, *S. rubicundus*, and natural hybrid song, although less actively to the F1 hybrid song. The results suggest that hybrid males may lose to males of parental species, whereas hybrid females would even have an advantage over parental females. Comparison of responses of females from allopatric populations and Mount Tomaros to different song types shows no evidence for reinforcement. Asymmetry found in female preferences may have implications for the structure of the hybrid zone. (c) 2013 The Linnean Society of London

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#### Detection of *Spiroplasma* and *Wolbachia* in the Bacterial Gonad Community of *Chorthippus parallelus*

Martinez-Rodriguez, P; Hernandez-Perez, M; Bella, JL. 2013

We have recently detected the endosymbiont *Wolbachia* in multiple individuals and populations of the grasshopper *Chorthippus parallelus* (Orthoptera: acrididae). This bacterium induces reproductive anomalies, including cytoplasmic incompatibility. Such incompatibilities may help explain the maintenance of two distinct subspecies of this grasshopper, *C. parallelus parallelus* and *C. parallelus erythropus*, which are involved in a Pyrenean hybrid zone that has been extensively studied for the past 20 years, becoming a model system for the study of genetic divergence and speciation. To evaluate whether *Wolbachia* is the sole bacterial infection that might induce reproductive anomalies, the gonadal bacterial community of individuals from 13 distinct populations of *C. parallelus* was determined by denaturing gradient gel electrophoresis analysis of bacterial 16S rRNA gene fragments and sequencing. The study revealed low bacterial diversity in the gonads: a persistent bacterial trio consistent with *Spiroplasma* sp. and the two previously described supergroups of *Wolbachia* (B and F) dominated the gonad microbiota. A further evaluation of the composition of the gonad bacterial communities was carried out by whole cell hybridization. Our results confirm previous studies of the cytological distribution of *Wolbachia* in *C. parallelus* gonads and show a homogeneous infection by *Spiroplasma*. *Spiroplasma* and *Wolbachia* cooccurred in some individuals, but there was no significant association of *Spiroplasma* with a grasshopper's sex or with *Wolbachia* infection, although subtle trends might be detected with a larger sample size. This information, together with previous experimental crosses of this grasshopper, suggests that *Spiroplasma* is unlikely to contribute to sex-specific reproductive anomalies; instead, they implicate *Wolbachia* as the agent of the observed anomalies in *C. parallelus*.

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#### Diverse reproductive barriers in hybridising crickets suggests extensive variation in the evolution and maintenance of isolation

Veen, T; Faulks, J; Tyler, F; Lloyd, J; Tregenza, T. 2013

Reproductive barriers reduce gene flow between populations and maintain species identities. A diversity of barriers exist, acting before, during and after mating. To understand speciation and coexistence, these barriers need to be quantified and their potential interactions revealed. We use the hybridising field crickets *Gryllus bimaculatus* and *G. campestris* as a model to understand the full complement and relative strength of reproductive barriers. We find that males of both species prefer conspecific females, but the effect is probably too weak to represent a barrier. In contrast, prezygotic barriers caused by females being more attracted to conspecific male song and preferentially mounting and mating with conspecifics are strong and asymmetric. Postzygotic barriers vary in direction; reductions in fecundity and egg viability create selection against hybridisation, but hybrids live longer than pure-bred individuals. Hybrid females show a strong preference for *G. bimaculatus* songs, which together with a complete lack of hybridisation by *G. campestris* females, suggests that asymmetric gene flow is likely. For comparison, we review reproductive barriers that have been identified between other Gryllids and conclude that multiple barriers are common. Different species pairs are separated by qualitatively different combinations of barriers, suggesting that reproductive isolation and even the process of speciation itself may vary widely even within closely related groups.

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#### Processing of acoustic signals in grasshoppers - A neuroethological approach towards female choice

Ronacher, B; Stange, N. 2013

Acoustic communication is a major factor for mate attraction in many grasshopper species and thus plays a vital role in a grasshopper's life. First of all, the recognition of the species-specific sound patterns is crucial for preventing hybridization with other species, which would result in a drastic fitness loss. In addition, there is evidence that females are choosy with respect to conspecific males and prefer or reject the songs of some individuals, thereby exerting a sexual selection on males. Remarkably, the preferences of females are preserved even under masking noise. To discriminate between the basically similar signals of conspecifics is obviously a challenge for small nervous systems. We therefore ask how the acoustic signals are processed and represented in the grasshopper's nervous system, to allow for a fine discrimination and assessment of individual songs. The discrimination of similar signals may be impeded not only by signal masking due to external noise sources, but also by intrinsic noise due to the inherent variability of spike trains. Using a spike train metric we could estimate how well, in principle, the songs of different individuals can be discriminated on the basis of neuronal responses, and found a remarkable potential for discrimination performance at the first stage, but not on higher stages of the auditory pathway. Next, we ask which benefits a grasshopper female may earn from being choosy. New results, which revealed correlations between specific song features and the size and immunocompetence of the males, suggest that females may derive from acoustic signals clues about condition and health of the sending male. However, we observed substantial differences between the preference functions of individual females and it may be particularly rewarding to relate the variations in female preferences to individual differences in the responses of identified neurons. (C) 2012 Elsevier Ltd. All rights reserved.

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#### Geographic variation in acoustic communication: reproductive character displacement and speciation

Gerhardt, HC. 2013

Background: Reproductive character displacement is a geographical pattern in which mate-attracting signals, preferences or both differ more in areas of sympatry than in areas of allopatry. Questions: What selective forces drive reproductive character displacement? What are its consequences? Methods: Reproductive character displacement in mate-attracting signals and/or female preferences are described for pairs of closely related field crickets (*Gryllus*), periodical cicadas (*Magicicada*), chorus and treefrogs (*Pseudacris* and *Hyla*), and tinkerbirds (*Pogoniulus*). These examples were characterized by data from multiple populations and evidence regarding the efficacy of sympatric divergence in signals or preferences. Conclusions: Whereas selection resulted in changes that reduce the production of genetically or behaviourally unfit hybrids in field crickets, chorus frogs, and green and grey treefrogs, reproductive character displacement in periodical cicadas and tinkerbirds was most likely driven by masking interference or mistakes in the identification of territorial rivals. Reproductive character displacement may not only accentuate or preserve divergence that arises in allopatry but can result in cascades of speciation if assortative mating arises between displaced and non-displaced populations.

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#### Taxonomic revision of the southern African genus *Pachyphymus* Uvarov, 1922 (Orthoptera: Acridoidea: Euryphyminae)

Bazelet, CS; Naskrecki, P. 2014



The southern African endemic genus, *Pachyphymus* Uvarov, 1922 (Orthoptera: Acrididae: Euryphyminae), is the only genus in the Euryphyminae subfamily with enlarged and hump-shaped pronotal crests. Here, we redescribe two species using newly evaluated diagnostic characters: *P. carinatus* Dirsh, 1956 and *P. cristulifer* (Serville, 1838); and describe two new species: *P. samwaysi* n. sp. and *P. namaquensis* n. sp. Of the 23 genera of Euryphyminae, *Pachyphymus* is arguably the most morphologically distinct. However, the species of *Pachyphymus*, like those of the other Euryphyminae, are difficult to distinguish morphologically because of a high degree of intraspecific variation. Height and shape of the pronotal crests and rugosity of the pronotum were previously considered diagnostic but are strongly variable within species. Degree of infumation of the hind wing is strongly conserved and is the single best diagnostic character in most cases. However, one population of *P. cristulifer*, which is isolated from the mainland population by a mountain range, shows very little conservation in this character. Additionally, one population of *P. namaquensis* and one population of *P. cristulifer*, both from outlying regions of their geographic range have intermediate wing infumation as well as other morphological characters. This may indicate recent or ongoing hybridization or divergence of the geographically overlapping species. This study emphasizes the need for molecular analysis to complement detailed morphological diagnosis of the species of Euryphyminae, a notoriously under-studied and taxonomically problematic group.

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#### **Wolbachia effects in natural populations of *Chorthippus parallelus* from the Pyrenean hybrid zone**

Zabal-Aguirre, M; Arroyo, F; Garcia-Hurtado, J; de La Torre, J; Hewitt, GM; Bella, JL. 2014

We evaluate for the first time the effect of *Wolbachia* infection, involving two different supergroups, on the structure and dynamics of the hybrid zone between two subspecies of *Chorthippus parallelus* (Orthoptera) in the Pyrenees. *Wolbachia* infection showed no effects on female fecundity or a slight increment in females infected by F supergroup, although in the last case it has to be well established. Cytoplasmic incompatibility (CI) is confirmed in crosses carried out in the field between individuals from a natural hybrid population. This CI, registered as the relative reduction in embryo production (sh), was of sh=0.355 and sh=0.286 in unidirectional crosses involving B and F supergroups, respectively. CI also occurred in bidirectional crosses (sh=0.147) but with a weaker intensity. The transmission rates of the two *Wolbachia* strains (B and F) were estimated by the optimization of a theoretical model to reach the infection frequencies observed in certain population. To fit this scenario, both supergroups should present transmission rates close to 1. Further, we have simulated the infection dynamics, and hence, the capacity of *Wolbachia* to structure the population of the host insects and to affect to reproduction and genetic introgression in the hybrid zone. This represents a first example of the influence of *Wolbachia* in an insect natural hybrid zone.

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#### **COURTSHIP SONG ANALYSIS IN TWO HYBRID ZONES BETWEEN SIBLING SPECIES OF THE CHORTHIPPUS ALBOMARGINATUS GROUP (ORTHOPTERA, GOMPHOCERINAE)**

Vedenina, VY. 2015

Two new hybrid zones between sibling species of the *Chorthippus albomarginatus* group were described on the basis of the courtship song analysis. Not only sound but also underlying stridulatory movements of hind legs were analyzed, which allowed classifying temporal parameters and conducting comparative analysis more reliably. One hybrid zone, between *Ch. albomarginatus* and *Ch. karelini*, was found in Uryanovsk and Samara regions of Russia. Another hybrid zone was found in Kherson region of Ukraine, around the reserved steppe Askaniya-Nova, presumably between *Ch. karelini* and *Ch. oschei*. A comparison of the natural and laboratory hybrids allowed suggesting the structure and fate of the hybrid zones.

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#### **Comparative cytogenetics of North Island tree weta in sympatry**

McKean, NE; Treweek, SA; Morgan-Richards, M. 2015

In North Island New Zealand three species of tree wet (*Hemideina*) have narrow regions of overlap. Using detailed measurements of chromosomes we compared the karyotypes of *Hemideina thoracica* with those of *Hemideina crassidens* and *Hemideina treweeki*. Although *H. thoracica* and *H. treweeki* have the same diploid number ( $2n=17$  [XO], 18 [XX]), distinct from *H. crassidens* ( $2n=15$  [XO] 16 [XX]); the karyotypes of *H. treweeki* and *H. crassidens* are more similar to each other than either is to *H. thoracica*. Elements within each karyotype were identified that are species specific and will aid identification of putative hybrids. Quantitative cytogenetics was used to identify the sex chromosome for *H. crassidens* and *H. treweeki*, which in contrast to previous inferences, is most likely the fifth-longest metacentric chromosome in *H. crassidens*, and the third-longest metacentric chromosome in *H. treweeki*.

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#### **Wide prevalence of hybridization in two sympatric grasshopper species may be shaped by their relative abundances**

Rohde, K; Hau, Y; Weyer, J; Hochkirch, A. 2015

Background: Hybridization between species is of conservation concern as it might threaten the genetic integrity of species. Anthropogenic factors can alter hybridization dynamics by introducing new potentially hybridizing species or by diminishing barriers to hybridization. This may even affect sympatric species pairs through environmental change, which so far has received little attention. We studied hybridization prevalence and the underlying behavioral mechanisms in two sympatric grasshopper species, a rare specialist (*Chorthippus montanus*) and a common generalist (*Chorthippus parallelus*). We conducted a mate choice experiment with constant intraspecific density and varying heterospecific density, i.e. varying relative frequency of both species. Results: Mate choice was frequency-dependent in both species with a higher risk of cross-mating with increasing heterospecific frequency, while conspecific mating increased linearly with increasing conspecific density. This illustrates that reproductive barriers could be altered by environmental change, if the relative frequency of species pairs is affected. Moreover, we performed a microsatellite analysis to detect hybridization in twelve syntopic populations (and four allotopic populations). Hybrids were detected in nearly all syntopic populations with hybridization rates reaching up to 8.9 %. Genetic diversity increased for both species when hybrids were included in the data set, but only in the common species a positive correlation between hybridization rate and genetic diversity was detected. Conclusion: Our study illustrates that the relative frequency of the two species strongly determines the effectiveness of reproductive barriers and that even the more choosy species (*Ch. montanus*) may face a higher risk of hybridization if population size decreases and its relative frequency becomes low compared to its sister species. The asymmetric mate preferences of both species may lead to quasi-unidirectional gene flow caused by unidirectional backcrossing. This might explain why genetic diversity increased only in the common species, but not in the rare one. Altogether, the hybridization rate was much higher than expected for a widely sympatric species pair.

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#### **Insect incidence and damage on pearl millet (*Pennisetum glaucum*) under various nitrogen regimes in Alabama**

Obeng, E; Cebert, E; Ward, R; Nyochembeng, LM; Mays, DA; Singh, HP; Singh, BP. 2015

Although pearl millet [*Pennisetum glaucum* (L.) R. Br.; Poales: Poaceae] is grown extensively on 5 continents and is attacked by various insects at all stages of growth and development, little is specifically known of how yields of this important crop are affected by insect herbivory. This study was conducted in north central Alabama to determine insect occurrence on pearl millet and to determine the levels of damage caused by insects feeding on pearl millet genotypes at different nitrogen rates. The field experiment was laid out following a randomized complete block design with 4 replications in which 4 genotypes and 4 fertilizer levels were arranged in factorial combinations. The pearl millet genotypes consisted of 2 open pollinated lines, '2304' and 'LHB08', and 2 hybrids, '606A1 2304' and '707A14280' and fertilization rates used were 0, 40, 80 and 120 kg ha<sup>-1</sup> N. Insect samplings were carried out weekly from 61 to 109 days after planting (DAP). Insects in 6 orders and



11 families were found on pearl millet genotypes. Eastern leaf-footed stinkbug (*Leptoglossus phyllopus* (L.); Hemiptera: Coreidae) was the most prevalent and dominant insect species found followed by the American bird grasshopper (*Schistocerca americana* Drury; Orthoptera: Acrididae) and the differential grasshopper (*Melanoplus differentialis* (Thomas; Orthoptera: Acrididae). Population of *L. phyllopus* was at its peak during the latter part of the growing season from 81 to 109 DAP. Populations of *S. americana* and *M. differentialis* declined as crop matured (61 DAP > 66 DAP > 75 DAP). Results also showed that leaf and head damage did not differ among genotypes and nitrogen rates tested.

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#### **Reproduction barrier between two lineages of bed bug (*Cimex lectularius*) (Heteroptera: Cimicidae)**

Wawrocka, K; Balvin, O; Bartonicka, T. 2015

Populations of bed bugs, *Cimex lectularius*, have increased in recent years spreading into numerous urban areas across the Western world and making them an increasingly important pest of the twenty-first century. Research into hybridization within and between different lineages of bed bugs can help us to understand processes of micro- and macro-evolution in these ectoparasites and may inform the control of this pest species. Hybridization experiments between two host lineages of bed bug (*C. lectularius*) from Central Europe (Czech Republic), those associated with humans and those with bats, were conducted under laboratory conditions. Number of eggs and early instars were compared between crosses of mixed host lineages (interspecific mating) with pairs from the same host lineage, those from the same locality and same lineage from different localities (intraspecific mating). While crosses within host lineages resulted in egg production and later instars, crosses between different host lineages were unsuccessful, although of the mated females possessed sperm in their mesospermales and/or seminal conceptacles. These crosses did not even result in egg production. Moreover, in the mixed lineage crosses, mortality rates in adults were higher (51 and 50 % higher in bat and human lineage, respectively) than in those animals from the same lineage. Survival of adults was in pairs from the same locality slightly higher than in pairs from different localities and differed statistically. These results support the existence of post-mating barriers and show reproductive isolation between two lineages of *C. lectularius*. Bat and human host adaptations can promote evolving of such barriers and can be product of alloxenic speciation.

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#### **Evolution of New Zealand insects: summary and prospectus for future research**

Buckley, TR; Krosch, M; Leschen, RAB. 2015

Knowledge on the evolution of the New Zealand insect fauna is reviewed and outstanding questions are highlighted. The New Zealand insect fauna is a composite of old and recent lineages and many spectacular examples of evolutionary processes are evident, including species radiations, hybridisation and unusual adaptations. We discuss the origins and evolution of four prominent communities within the insect fauna: terrestrial lowland insects, alpine insects, aquatic insects and insect communities from offshore islands. Within each of these communities, significant lineages are discussed, and in particular the crucial adaptations that enable these lineages to thrive and diversify. Glacial history has had a dramatic impact on the New Zealand insects, and the effects on different lineages are discussed. The New Zealand insects are unique, yet many are threatened with extinction, and efforts to preserve the fauna are reviewed. Despite the accumulating knowledge, major gaps still exist and these are outlined, as are opportunities to address key questions. The review concludes with a synthesis and a discussion of how systematics, new technologies and integrative approaches have the promise to improve dramatically our understanding of New Zealand insect evolution.

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#### **Speciation Progress: A Case Study on the Bushcricket *Poecilimon veluchianus***

Eweleit, L; Reinhold, K; Sauer, J. 2015

Different mechanisms such as selection or genetic drift permitted e.g. by geographical isolation can lead to differentiation of populations and could cause subsequent speciation. The two subspecies of *Poecilimon veluchianus*, a bushcricket endemic to central Greece, show a parapatric distribution and are partially reproductively isolated. Therefore, *P. veluchianus* is suitable to investigate an ongoing speciation process. We based our analysis on sequences of the internal transcribed spacer (ITS) and the mitochondrial control region (CR). The population genetic analysis based on the nuclear marker ITS revealed a barrier to gene flow within the range of *Poecilimon veluchianus*, which corresponds well to the described subspecies. In contrast to the results based on the nuclear ITS marker, the mitochondrial CR marker does not clearly support the separation into two subspecies with restricted gene flow and a clear contact zone. Furthermore, we could identify isolation by distance (IBD) as one important mechanism responsible for the observed genetic structure (based on the ITS marker). The population genetic analysis based on the nuclear marker ITS also suggests the existence of hybrids in the wild. Furthermore, the simultaneous lack of strong prezygotic barriers and the presence of postzygotic mating barriers, observed in previous laboratory experiments, suggest that a secondary contact after an allopatric phase is more likely than parapatric speciation.

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#### **First evidence of *Wolbachia* infection in populations of grasshopper *Podisma sapporensis* (Orthoptera: Acrididae)**

Bugrov, AG; Ilinsky, YY; Strunov, A; Zhukova, M; Kiseleva, E; Akimoto, S; Tatsuta, H. 2016

The brachypterous grasshopper *Podisma sapporensis* (Orthoptera: Acrididae) is distributed throughout the Sakhalin, Kunashir and Hokkaido Islands. Karyotypes of this species consist of two major chromosomal races with different sex chromosome systems, XO/XX and XY/XX. Molecular phylogeographic analysis of the chromosome races and subraces confirms the genetic divergence of the races and subraces in *P. sapporensis*. Here we first report that *P. sapporensis* is infected with *Wolbachia* consisting of three variants on *wsp* locus, while *gatB* locus was monomorphic. Furthermore, observation of cell tissue of *P. sapporensis* using electron microscopy confirmed the infection of *Wolbachia* that was inferred from polymerase chain reaction and revealed the distribution of the bacteria in the head, thorax and abdomen of *P. sapporensis* embryos. Our finding may shed new light on *Wolbachia* as a possible agent causing hybrid dysfunction resulting from experimental crosses between chromosome races or subraces of *P. sapporensis*.

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#### **Reinforcement and a cline in mating behaviour evolve in response to secondary contact and hybridization in shield-back katydids (Orthoptera: Tettigoniidae)**

Cole, JA. 2016

In a dispersal-limited species that has evolved reproductive character displacement at a contact zone, a cline in mating behaviour may result if gene flow diffuses alleles out of the contact zone into allopatric populations. Prior work has found such a clinal pattern in the shield-back katydid *Aglaothorax morsei*, in which the male calling songs in a sympatric population have a displaced, short interpulse interval that increases in length with increasing distance from the contact zone. In this study, molecular phylogenetic and female preference data show that (1) sympatric populations result from secondary contact, (2) hybridization in sympatry has resulted in unidirectional mitochondrial introgression and (3) female preferences are consistent with reproductive character displacement and could generate a cline in mating behaviour. These data together suggest a history of reinforcement, generally considered rare in acoustically communicating insects; thus, *Aglaothorax* represents an important example of a rarely documented evolutionary process.

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## Little or no gene flow despite F-1 hybrids at two interspecific contact zones

McKean, NE; Trewick, SA; Morgan-Richards, M. 2016

Hybridization can create the selective force that promotes assortative mating but hybridization can also select for increased hybrid fitness. Gene flow resulting from hybridization can increase genetic diversity but also reduce distinctiveness. Thus the formation of hybrids has important implications for long-term species coexistence. This study compares the interaction between the tree weta *Hemideina thoracica* and its two neighboring species; *H. crassidens* and *H. trewicki*. We examined the ratio of parent and hybrid forms in natural areas of sympatry. Individuals with intermediate phenotype were confirmed as first generation hybrids using nine independent genetic markers. Evidence of gene flow from successful hybridization was sought from the distribution of morphological and genetic characters. Both species pairs appear to be largely retaining their own identity where they live in sympatry, each with a distinct karyotype. *Hemideina thoracica* and *H. trewicki* are probably reproductively isolated, with sterile F-1 hybrids. This species pair shows evidence of niche differences with adult size and timing of maturity differing where *Hemideina thoracica* is sympatric with *H. trewicki*. In contrast, evidence of a low level of introgression was detected in phenotypes and genotypes where *H. thoracica* and *H. crassidens* are sympatric. We found no evidence of size divergence although color traits in combination with hind tibia spines reliably distinguish the two species. This species pair show a bimodal hybrid zone in the absence of assortative mating and possible sexual exclusion by *H. thoracica* males in the formation of F-1 hybrids.

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## ACOUSTIC SIGNALS IN INSECTS: A REPRODUCTIVE BARRIER AND A TAXONOMIC CHARACTER

Tishechkin, DY; Vedenina, VY. 2016

In singing insects, the song is an important component of the specific mate recognition system (SMRS). In communities of sympatric singing species, there is a partitioning of communication channels, the so-called "acoustic niches". Within one community, the songs of different species always differ in temporal or frequency characters, i.e. occupy different acoustic niches. However, conspecific songs do not always act as an inter specific reproductive barrier, despite always being a SMRS component. The species that do not communicate acoustically due to either allopatry or a different timing of vocalization, or inhabiting different biotopes, or unmatched food specializations can sing similar songs, thus forming reproductively isolated communities. Individuals of the opposite sex not only need to recognize a conspecific mate, but also have to evaluate its "quality". A close-range signal (courtship song) provides more opportunities for a choice of the "best" male than does a distant signal (calling song). In many species of Orthoptera, courtship includes not only acoustic, but also vibration, visual, chemical and mechanical signals. An analysis of cricket songs showed that, on average, the courtship songs are more elaborate and more variable than the calling songs. At the same time, due to the difference in mating behaviour between grasshoppers and crickets, the acoustic component of courtship is used for an evaluation of mate quality to a greater extent in the fowler than it is in the latter group. Courtship songs of grasshoppers are generally more elaborate in temporal structure than cricket songs and, moreover, can be accompanied by visual displays such as movements of various parts of the body. Thus, song evolution in grasshoppers is more driven by sexual selection than that of crickets. According to the reinforcement hypothesis, a premating barrier between hybridizing species becomes stronger in response to reduced hybrid fitness. However, our behavioural experiments conducted on two groups of hybridizing grasshopper species did not confirm the reinforcement hypothesis. We explain this firstly, by a low level of genetic incompatibility between the hybridizing species and secondly, by high hybrid fitness when attracting a mate. A high competitive capability of hybrids might be accounted for by the attractiveness for females of new elements in hybrid courtship songs. When we divide similar forms on the basis of songs, we distinguish biological species using their reproductive isolation as a criterion. Acoustic differences between species are usually greater than morphological ones. Therefore, analyzing the song allows us to find out the real status of doubtful taxa of species rank, to distinguish species in a flock of sibling forms and to reveal cryptic species in the cases when morphological studies fail to provide a univocal result. At the same time, songs have intra-specific variability and its range can be different in various groups. Therefore, it is necessary to study which degree of difference corresponds to the species level before interpreting the status of some forms based on song comparisons. Besides this, song similarities cannot be evidence that acoustically isolated forms are conspecific. On the other hand, song differences between these forms prove that they are full-rank species.

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## Variation in complex mating signals in an "island" hybrid zone between *Stenobothrus* grasshopper species

Sradnick, J; Klopfel, A; Elsner, N; Vedenina, V. 2016

Two grasshopper species *Stenobothrus rubicundus* and *S. clavatus* were previously shown to meet in a narrow hybrid zone on Mount Tomaros in northern Greece. The species are remarkable for their complex courtship songs accompanied by conspicuous movements of antennae and wings. We analyzed variations in forewing morphology, antenna shape, and courtship song across the hybrid zone using a geographic information system, and we documented three contact zones on Mount Tomaros. All male traits and female wings show abrupt transitions across the contact zones, suggesting that these traits are driven by selection rather than by drift. Male clines in antennae are displaced toward *S. clavatus*, whereas all clines in wings are displaced toward *S. rubicundus*. We explain cline discordance as depending on sexual selection via female choice. The high covariance between wings and antennae found in the centers of all contact zones results from high levels of linkage disequilibria among the underlying loci, which in turn more likely results from assortative mating than from selection against hybrids. The covariance is found to be higher in *clavatus*-like than *rubicundus*-like populations, which implies asymmetric assortative mating in parental-like sites of the hybrid zone and a movement of the hybrid zone in favor of *S. clavatus*.

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## ADDITIONS AND CORRECTIONS TO THE CADASTRE OF ORTHOPTERA INSECTS OF SAMARSKAYA LUKA, ON THE BASIS OF ANALYSIS OF ACOUSTIC SIGNALS OF MALES

Benediktov, AA. 2017

For the territory of Samarskaya Luka, at the village Bakhilova Polyana (I.I. Sprygin Zhiguli State Natural Biosphere Reserve), 25 species of Orthoptera were found in mid-July 2016. These species were identified basically by the analysis of male acoustic signals. This is 44% of the total species composition of Samarskaya Luka Orthoptera, specified in the Cadastre of invertebrates of Samarskaya Luka. The specimens belonging to the grasshopper *Platychleis albopunctata* (= *P. intermedia* auct.) are clarified. The cricket *Melanogryllus desertus* and the locust *Chorthippus dorsatus* were found for the first time in the Samarskaya Luka. The species composition of the cryptic taxa of the << *Chorthippus biguttulus* group >> of the Middle Volga region is discussed. Based on the unstable amplitude-time structure of the signals of the supposed *Ch. biguttulus* males from Malaya Bahilova Mountain, it is assumed that they may have a hybrid origin.

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## DNA barcoding of crickets, katydids and grasshoppers (Orthoptera) from Central Europe with focus on Austria, Germany and Switzerland

Hawlitshchek, O; Moriniere, J; Lehmann, GUC; Lehmann, AW; Kropf, M; Dunz, A; Glaw, F; Detcharoen, M; Schmidt, S; Hausmann, A; Szucsich, NU; Caetano-Wyler, SA; Haszprunar, G. 2017

We present a DNA barcoding study on the insect order Orthoptera that was generated in collaboration between four barcoding projects in three countries, viz. Barcoding Fauna Bavarica (Germany), German Barcode of Life, Austrian Barcode of Life and Swiss Barcode of Life. Our data set includes 748 COI sequences from 127 of the 162 taxa (78.4%) recorded in the three countries involved. Ninety-three of these 122 species (76.2%, including all Ensifera) can be reliably identified using DNA barcodes. The remaining 26 caeliferan species (families Acrididae and Tetrigidae) form ten clusters that share barcodes among up to five species, in three cases even across different genera, and in six cases even sharing individual barcodes. We discuss incomplete lineage sorting and hybridization as most likely causes of this phenomenon, as the species concerned are phylogenetically young and hybridization has been previously observed. We also highlight the problem of nuclear

mitochondrial pseudogenes (numts), a known problem in the barcoding of orthopteran species, and the possibility of Wolbachia infections. Finally, we discuss the possible taxonomic implications of our barcoding results and point out future research directions.

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#### **Male tree weta are attracted to cuticular scent cues but do not discriminate according to sex or among two closely related species**

Wehi, PM; Monks, A; Morgan-Richards, M. 2017

Recognition of conspecifics is an essential precursor of successful mating. Where related species coexist, species discrimination might be important, but because related species are similar, species signal recognition may actually be low. Chemical cues such as cuticular hydrocarbons (CHCs) are frequently used by insects to identify suitable sexual partners. We predicted that New Zealand tree weta (*Hemideina* spp.), a genus of nocturnal ensiferan Orthoptera that live both allopatrically and sympatrically, use chemical signals from either frass or CHCs to find mates. In a series of six laboratory trials using both *H. thoracica* and *H. crassidens*, we found that male tree weta, but not female tree weta, occupied cavities primed with female cuticular cues more often than cavities without. However, males did not discriminate between chemical cues of male and female conspecifics, or between conspecifics and heterospecifics. In field trials, tree weta did not occupy artificial cavities primed with either female frass or female cuticular cues more often than unscented cavities. However, in both trials weta preferentially returned to cavities that had already been occupied earlier in the trials. A final field trial confirmed the presence of mixed species harems during the mating season in one region of sympatry. Our results suggest that selection on sex and species specific chemical cues that could be used to find conspecific mates is weak. Mixed species aggregations suggest that identification of conspecific mating cues has not evolved to be species specific. We infer that for male tree weta, the cost of mating with heterospecifics is likely less than not mating at all.

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#### **Climatic effects on population declines of a rare wetland species and the role of spatial and temporal isolation as barriers to hybridization**

Rohde, K; Hau, Y; Kranz, N; Weinberger, J; Elle, O; Hochkirch, A. 2017

Climate change and climatic extremes may affect species directly or indirectly. While direct climatic effects have been intensively studied, indirect effects, such as increasing hybridization risk, are poorly understood. The goal of our study was to analyse the impact of climate on population dynamics of a rare habitat specialist, *Chorthippus montanus*, as well as the fine-scale spatial overlap with a sympatric habitat generalist, *Chorthippus parallelus* and the dispersion of hybrids. We were particularly interested in the role of spatiotemporal overlap on heterospecific encounter frequencies. We conducted high-precision mark-recapture studies on two sites over 7 years and genotyped 702 individuals of two *C. montanus* generations to detect hybrids. We tested the performance of three programs (structure, newhybrids and adegenet) and accepted only hybrids detected by the two best performing programs. We then tested for correlations between yearly population trends and climatic variables. Furthermore, we analysed the spatial dispersion of both taxa and the hybrids to calculate variation in spatial and temporal overlap and infer heterospecific encounter probabilities. Our results revealed that droughts during the egg phase and rainy weather during nymphal development were strongly correlated with population declines in the habitat specialist. The highest hybridization rate (196%) was found in the population with lowest population size. The combined effects of spatial and temporal niche overlap decreased heterospecific encounter probabilities to 42-76% compared to 20-28% and 11-19% calculated alone from phenology or spatial overlap respectively. Hybrids were detected in areas of higher heterospecific encounter probability, mainly at the edge of the specialists' occupied habitat in areas with intermediate soil moisture conditions compared to the parental species. This illustrates that the combination of spatial and temporal segregation provides an effective barrier to hybridization. However, the high hybridization rate in one of the populations suggests that this function may decrease with decreasing population size. This supports the hypothesis that climatic extremes threaten rare species directly by reducing reproductive success and may indirectly increase hybridization risk. A is available for this article.

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#### **Components of reproductive isolation between the closely related grasshopper species *Chorthippus biguttulus* and *C. mollis***

Finck, J; Ronacher, B. 2017

The formation and maintenance of species in nature is accomplished by the evolution of reproductive isolating mechanisms. To understand patterns of speciation and coexistence between species, it is crucial to obtain a complete synopsis of reproductive isolating barriers. We identified multiple reproductive isolation barriers between two closely related species, *Chorthippus biguttulus* and *Chorthippus mollis*, and quantified their respective contributions to isolation. To this end, we produced hybrids and backcrosses in the laboratory to examine reproductive isolation at multiple stages in the life history. The prezygotic barriers, based on chemical and acoustic cues, are currently the strongest impediments to gene flow between *C. biguttulus* and *C. mollis*. This indicates an important role for sexual selection in the maintenance of species isolation. However, extrinsic and intrinsic postzygotic isolation barriers also contributed to reproductive isolation. The virtual sterility of F1 hybrid males was based on both the dysfunctionality of their testes and intermediate behavioral mating traits (behavioral sterility). This study demonstrates that a cascade of reproductive isolating mechanisms reduces the gene flow between *C. biguttulus* and *C. mollis*. Our results further demonstrate that the courtship display in these species consists of multimodal signals and indicates a key role of chemical cues in reproductive isolation and speciation in grasshoppers.

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#### **Divergent mechanisms of acoustic mate recognition between closely related field cricket species (*Teleogryllus* spp.)**

Bailey, NW; Moran, PA; Hennig, RM. 2017

Effective recognition of conspecific mating signals reduces the risk of maladaptive hybridization. Dissecting the signal recognition algorithms that underlie preferences is a useful approach for testing whether closely related taxa evaluate the same or different signal features to achieve mate recognition. Such data provide information about potential constraints and targets of selection during evolutionary divergence. Using a series of mate choice trials, we tested whether closely related, but genetically and phenotypically divergent, field cricket species (*Teleogryllus oceanicus* and *Teleogryllus commodus*) use shared or distinct recognition algorithms when evaluating acoustic male calling songs. These species overlap in sympatry, show premating isolation based on female discrimination of male calling songs, yet are capable of producing hybrid offspring. Unexpectedly, female selectivity for features of male song differed between the two species. We found that the two species use a combination of shared and unique signal filtering mechanisms, and we characterized how information about male carrier frequency, pulse rate and temporal patterning is integrated to achieve song recognition in each species. These results illustrate how comparatively few, simple modifications in key components of signal recognition algorithms can lead to striking interspecific discrimination between closely related taxa, despite apparent signal complexity. The finding that some steps during signal recognition and filtering are shared between the species, while others differ, can help to identify behavioural traits targeted by selection during evolutionary divergence. (C) 2017 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

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#### **New application method for entomopathogenic nematode *Heterorhabditis bacteriophora* (Poinar, 1976) (Rhabditida: Heterorhabditidae) HBH strain against *Locusta migratoria* (Linnaeus, 1758) (Orthoptera: Acrididae)**

Sahin, YS; Bouhari, A; Ulu, TC; Sadic, B; Susurluk, IA. 2018

Entomopathogenic nematodes (EPNs) of the families Heterorhabditidae and Steinernematidae are being used as biocontrol agents against many soil borne insect pests in agriculture. Above-ground applications against the insects are usually unsuccessful due to the lack of humidity. Therefore, EPNs rapidly lose their effectiveness. In this study, conducted in 2018 under laboratory conditions in Bursa-Turkey, a new application method was developed for the use of *Heterorhabditis*

bacteriophora (Poinar, 1976) (Rhabditida: Heterorhabditidae) HBH hybrid strain against the migratory locust, *Locusta migratoria* (Linnaeus, 1758) (Orthoptera: Acrididae). A new trap system is coated with hydrophilic cotton fabric to provide the necessary humidity to allow the use of EPNs above-ground. Three different application rates of *H. bacteriophora* (5000, 25000 and 50000 IJs) were applied to the trap system. The fabric was inoculated with the nematodes and combined with a reservoir containing 200 ml of ringer solution. The dead and live nematodes were recorded periodically to determine their persistence on the fabric. The mortality of *L. migratoria* were also recorded to determine the infectivity of *H. bacteriophora*. The infectivity and persistence of the nematodes was sustained for more than 4 weeks by this method.

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#### **Karyotype Variability and Inter-Population Genomic Differences in Freshwater Ostracods (Crustacea) Showing Geographical Parthenogenesis**

Symonova, R; Vrbova, I; Lamatsch, DK; Paar, J; Matzke-Karasz, R; Schmit, O; Martens, K; Muller, S. 2018

Transitions from sexual to asexual reproduction are often associated with polyploidy and increased chromosomal plasticity in asexuals. We investigated chromosomes in the freshwater ostracod species *Eucypris virens* (Jurine, 1820), where sexual, asexual and mixed populations can be found. Our initial karyotyping of multiple populations from Europe and North Africa, both sexual and asexual, revealed a striking variability in chromosome numbers. This would suggest that chromosomal changes are likely to be accelerated in asexuals because the constraints of meiosis are removed. Hence, we employed comparative genomic hybridization (CGH) within and among sexual and asexual populations to get insights into *E. virens* genome arrangements. CGH disclosed substantial genomic imbalances among the populations analyzed, and three patterns of genome arrangement between these populations: 1. Only putative ribosomal DNA (rDNA)-bearing regions were conserved in the two populations compared indicating a high sequence divergence between these populations. This pattern is comparable with our findings at the interspecies level of comparison; 2. Chromosomal regions were shared by both populations to a varying extent with a distinct copy number variation in pericentromeric and presumable rDNA-bearing regions. This indicates a different rate of evolution in repetitive sequences; 3. A mosaic pattern of distribution of genomic material that can be explained as non-reciprocal genetic introgression and evidence of a hybrid origin of these individuals. We show an overall increased chromosomal dynamics in *E. virens* that is complementary with available phylogenetic and population genetic data reporting highly differentiated diploid sexual and asexual lineages with a wide variety of genetic backgrounds.

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#### **Anthropogenic cause of range shifts and gene flow between two grasshopper species revealed by environmental modelling, geometric morphometrics and population genetics**

Sivyer, L; Morgan-Richards, M; Koot, E; Trewick, SA. 2018

The range of a species is controlled by biotic and abiotic factors; both could have changed recently due to human activity. We used environmental modelling, morphometric and genetic data to interpret ecological responses at the species boundary of a pair of New Zealand grasshoppers with very different ranges; one widespread (*Phaulacridium marginale*) and one restricted to semi-arid central/southern South Island (*Phaulacridium otagoense*). Climate- and habitat-based distribution models for grasshoppers in the past (last glacial maximum), present and future (2070), in concert with modelling of vegetation patterns imply range and demographic expansion of *P. marginale* and stability of *P. otagoense*. mtDNA sequence revealed four main lineages with pronounced differences in genetic diversity and geographical range. The widespread lineage associated with *P. marginale* revealed a signature of range expansion but regionally restricted lineages were geographically structured at a fine scale. Within the narrow geographical range of *P. otagoense*, three mtDNA lineages resulted in high diversity, more typical of large stable populations. Geometric analysis of pronotum shape identified individuals from a region of sympatry with mixed characteristics. Mismatch of phenotype, mtDNA lineage and nuclear DNA sequence indicates introgression between grasshopper species now in contact. This appears to be accompanied by *P. otagoense* range reduction through ecological competition. Deforestation by people starting approximate to 800 years ago best explains range change and resulting hybridisation of these grasshoppers. Anthropogenic habitat modification can have indirect consequences on insect biodiversity and conservation by enabling introgression between formerly separate populations and species.

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#### **Chorthippus parallelus and Wolbachia: Overlapping Orthopteroid and Bacterial Hybrid Zones**

Martinez-Rodriguez, P; Bella, JL. 2018

*Wolbachia* is a well-known endosymbiotic, strictly cytoplasmic bacterium. It establishes complex cytonuclear relations that are not necessarily deleterious to its host, but that often result in reproductive alterations favoring bacterial transmission. Among these alterations, a common one is the cytoplasmic incompatibility (CI) that reduces the number of descendants in certain crosses between infected and non-infected individuals. This CI induced by *Wolbachia* appears in the hybrid zone that the grasshoppers *Chorthippus parallelus parallelus* (Cpp) and *C. p. erythropus* (Cpe) form in the Pyrenees: a reputed model in evolutionary biology. However, this cytonuclear incompatibility is the result of sophisticated processes of the co-divergence of the genomes of the bacterial strains and the host after generations of selection and coevolution. Here we show how these genome conflicts have resulted in a finely tuned adjustment of the bacterial strain to each pure orthopteroid taxon, and the striking appearance of another, newly identified recombinant *Wolbachia* strain that only occurs in hybrid grasshoppers. We propose the existence of two superimposed hybrid zones: one organized by the grasshoppers, which overlaps with a second, bacterial hybrid zone. The two hybrid zones counterbalance one another and have evolved together since the origin of the grasshopper's hybrid zone.

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#### **The matchstick grasshopper genus *Warramaba* (Morabidae: Morabinae): a description of four new species and a photographic guide to the group**

Kearney, MR. 2018

Matchstick grasshoppers are a unique and diverse element of Australia's insect fauna with great potential as a model system for ecological, evolutionary and biogeographical studies. The genus *Warramaba* comprises four bisexual species. It is of special interest from an evolutionary point of view because two parthenogenetic lineages (the Standard and Boulder-Zanthus phylads of *W. virgo*) have evolved through hybridization events between two of the sexual species. Despite the extensive genetic and systematic work that has been done on this genus, three of the bisexual species are yet to be formally named (P196, P169 and P125) and no key exists for their identification. Here I formally describe these species, respectively, as *W. whitei* sp. nov., *W. flavolineata* sp. nov. and *W. grandis* sp. nov. and split the parthenogenetic species *W. virgo* into two distinct species (the addition of *W. ngadju* sp. nov.). I also provide a photographic guide and key to the identification of all species in the genus.

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#### **Dominance effects strengthen premating hybridization barriers between sympatric species of grasshoppers (Acrididae, Orthoptera)**

Gottsberger, B; Mayer, F. 2019

Sexual selection can lead to the rapid evolution of premating hybridization barriers and allows accelerated diversification and speciation within an evolutionary lineage. Especially during early stages of divergence, hybridization may impede further divergence, which strongly depends on the reproductive success of hybrids. Behavioural sterility of hybrids can limit or even prevent homogenizing gene flow. In this study, we investigated the attractiveness of male courtship songs for females of the grasshopper species *Chorthippus biguttulus* and *C. brunneus* and their interspecific F1 and F2 hybrids. Song preferences of females of both species are highly species specific and differ in three parameters: shape of the preference function, preference for syllable pattern and phrase duration. F1 hybrid females of

both reciprocal crosses as well as F2 hybrid females resembled closely pure *C. biguttulus* females in respect of shape of the preference function and preference for syllable pattern, while preference for phrase duration showed an intermediate expression. This resulted in song preferences of hybrid females that closely resembled those of one parental species, that is *C. biguttulus* females. Such strong dominance effects were rarely reported so far. They represent an effective barrier limiting gene flow between the two species, since hybrid females will backcross to only one parental species and discriminate against hybrid males, which are behaviourally sterile. Such taxon-specific modes of inheritance may have facilitated the rapid divergence of acoustically communicating grasshoppers of the species group of *Chorthippus biguttulus*. Our findings have novel implications on the expression of neuronal filters and the evolution of complex courtship signals.

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#### **Crickets of the genus *Gryllus* in the United States (Orthoptera: Gryllidae: Gryllinae)**

Weissman, DB; Gray, DA. 2019

*Gryllus* field and wood crickets of the United States, mostly west of the Mississippi River, are reviewed and revised. We validate the following 18 *Gryllus* cricket names: *G. armatus*, *G. assimilis*, *G. brevicaudus*, *G. cayensis*, *G. coxii*, *G. firmus*, *G. fulvipes*, *G. integer*, *G. lineaticeps*, *G. multipulsator*, *G. ovisopis*, *G. pennsylvanicus*, *G. personatus*, *G. rubens*, *G. texensis*, *G. veletis*, *G. vernalis*, and *G. vocalis*. We synonymize *G. alogus* under *G. vocalis*. We designate a lectotype for *G. armatus*. We describe the following 17 new *Gryllus* species: *G. chisosensis*, *G. leei*, *G. lightfooti*, *G. longicercus*, *G. makhsosica*, *G. montis*, *G. navajo*, *G. planeta*, *G. regularis*, *G. saxatilis*, *G. sotol*, *G. staccato*, *G. thinos*, *G. franspecos*, *G. veintinueve*, *G. veletisoides*, and *G. vulcanus*. We present biology, distribution, and genetic analysis of all taxa and discuss their nearest relatives.

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#### **Cytomolecular analysis of the male sex chromosome of *Tropidacris cristata grandis* (Thunberg, 1824) (Orthoptera: Romaleidae)**

Baldissera, JNC; Pine, MB; Lopes, TBF; Dias, FC; de Domenico, FC; da Rosa, R. 2019

Many species of grasshopper have an XX/XO sex chromosome system, including *Tropidacris cristata grandis* (23, XX/XO). The X chromosome behaves differently from the autosomes, but little is known about its origin and molecular composition. To better understand the genomic composition and evolutionary processes involved in the origin of the sex chromosomes, we undertook an analysis of its meiotic behavior, heterochromatin distribution and microdissection in *T. c. grandis*. Analysis of meiotic cells revealed a difference in the behavior of the X chromosome compared to the autosomes, with different patterns of condensation and cellular arrangement. Heterochromatic terminal blocks were predominant. The chromosome painting revealed a bright block in the centromeric/pericentromeric region of the X chromosome and slight markings in the other regions. In the autosomes, the X chromosome probe hybridized in the centromeric/pericentromeric region, and hybridization signals on terminal regions corresponding to the heterochromatic regions were also observed. The results showed that the X chromosome contains a significant amount of repetitive DNA. Based on the hybridization pattern, it is possible that the autosomes and sex chromosomes of *T. c. grandis* have a similar composition of repetitive DNAs, which could mean that the X chromosome has an autosomal origin.

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#### **Inter-geographic hybridization in the corn borer *Ostrinia furnacalis* reduced the fitness of hybrids**

He, HM; Tang, JJ; Huang, LL; Gao, YL; Xue, FS. 2019

It is commonly observed that if the genetic divergences between parental lineages are too marked, the intermixed offspring might not be successful or might present reduced fitness, i.e., hybrid inferiority. In the present study, we performed an intraspecific hybridization using two populations of the Asian corn borer, *Ostrinia furnacalis*: a southern population (S) from Huizhou city (23.09 degrees N, 114.4 degrees E) and a northern population (N) from Harbin city (44.9 degrees N, 127.2 degrees E). The key life-history traits were compared between the two populations with geographical reproductive isolation and their two hybrid populations (SfxNo and NfxSo populations) at 20, 24, 28 and 32 degrees C. Our results showed that there were significant differences in life-history traits in the two parental populations, with the S population performing better. However, the two hybrid populations exhibited delayed larval development time, relatively reduced body weight, lower growth rate and sex ratio distortion compared with their parents. Our results provided further evidence that intraspecific hybridization between the two geographical populations reduced the fitness of the hybrids. The sexual size dimorphism was also different between the pure populations and the hybrid populations. We also found that the sex ratios in the two hybrid populations were mainly influenced by the genotype of the mothers. The negative effects of intraspecific hybridization on the key life-history traits may provide a genetic means of pest management to suppress pest populations.

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#### **Pleistocene origins of chorusing diversity in Mediterranean bush-cricket populations (*Ephippiger diurnus*)**

Esquer-Garrigos, Y; Streiff, R; Party, V; Nidelet, S; Navascues, M; Greenfield, MD. 2019

We studied the Pleistocene diversification of a relatively endemic Mediterranean insect (*Ephippiger diurnus*; Orthoptera: Tettigoniidae) to understand how species with restricted range may nonetheless exhibit the complex phylogeography normally associated with broad distribution. A time-calibrated molecular phylogeny based on two mitochondrial genes showed that *E. diurnus* diverged into two major clades, distinguished largely by male song, before or early during the Pleistocene. Several subclades also diverged before the most recent glacial period. Data from 20 microsatellite loci indicated higher genetic diversity in populations along the Mediterranean coast in France, consistent with the hypothesis that glacial refuges were located there. Isolation by distance' accounts for much genetic differentiation between populations, but some adjacent populations are highly differentiated. A Bayesian approach defined genetically distinct clusters and assigned individuals to their most probable cluster. Clusters corresponded to clades in the phylogenetic tree, and we used cluster assignments to estimate interclade gene flow in areas of potential secondary contact. Gene flow is negligible in potential contact areas in the Pyrenees, but a narrow hybrid zone featuring a steep cline exists on the coast. This hybrid zone suggests that the major clades represent distinct species that diverged within a restricted area during the Pleistocene.

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#### **Does hunger lead to hybridization in a genus of sexually cannibalistic insects (Orthoptera: Prophalangopsidae)?**

Dupuis, JR; Judge, KA; Brunet, BMT; Chan, SO; Sperling, FAH. 2020

Allochronic isolation can be a strong mechanism for reproductive isolation and speciation. However, imperfect allochrony and the expression of phenological plasticity can erode temporal barriers to gene flow and result in hybridization between divergent lineages. Here, we combine behavioural ecology and genomics to investigate this scenario in two closely related species of grigs in the genus *Cyphoderris*. These species exhibit a unique mating system whereby females feed on the fleshy hind wings of the male during copulation, and copulation with conspecific males is more likely in food-restricted females than in well-fed females. In western Canada, *Cyphoderris buckelli* and *Cyphoderris monstrosa* are sympatric but largely allochronically separated, with *C. buckelli* breeding earlier. However, their breeding seasons can overlap, leading to potential for older *C. buckelli* females to mate with young *C. monstrosa* males to obtain resources via sexual cannibalism. We used behavioural assays to test whether female feeding status affects the propensity for interspecific mating between *C. buckelli* females and *C. monstrosa* males. We then tested for hybridization and gene exchange in wild populations of both species, using morphology, mitochondrial DNA and genome-wide nuclear markers. We found that interspecific courtship and mating can occur, but the relationship between food restriction and increased propensity for hybridization was not significant. Although we observed intraspecific population genetic structure in both species, we found no signatures of hybridization in the morphological or genetic datasets, which suggests that postmating reproductive barriers might be preventing successful hybridization in the wild.



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## Source Areas and Migratory Trajectories of *Locusta migratoria migratoria* (Orthoptera: Acrididae) in the Border Region of Tacheng, Xinjiang, China and Adjacent Regions

Yu, BJ; Mai, JW; Chen, X; Xu, CY; Chen, Y; Cao, KL; Xu, Y; Roman, J; Ji, R. 2020

The Hybrid Single Particle Lagrangian Integrated Trajectory Model and meteorological graphics software (Grads and ArcGIS) were used to analyze source areas and migratory trajectories of a population of *Locusta migratoria migratoria* (L.) (Orthoptera: Acrididae) in the Tacheng region of Xinjiang, China that borders with eastern Kazakhstan. The source areas of these locusts migrating into the Tacheng region are distributed near Lake Alakol, Lake Zaisan, eastern Lake Balkhash, the Irtysh River, and Ayaguz River in Kazakhstan. Locusts follow nine migratory trajectories in their invasion of Tacheng. On the respective migration dates, a westerly wind, northerly wind, or northwesterly wind, the latter being the prevailing wind direction, occurred at 950 hPa over the source areas. At migration heights of 300, 500, and 800 m above mean sea level, the air temperatures ranged from 25.0-31.0 degrees C, 21.5-26.0 degrees C, and 21.0-25.0 degrees C, respectively. The concept of insect migration pattern in Central Asia is proposed, but a series of theoretical and empirical studies will be needed to provide support for this postulation.

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## Multilocus phylogeny of *Gryllus* field crickets (Orthoptera: Gryllidae: Gryllinae) utilizing anchored hybrid enrichment

Gray, DA; Weissman, DB; Cole, JA; Lemmon, EM; Lemmon, AR. 2020

We present the first comprehensive molecular phylogeny of *Gryllus* field cricket species found in the United States and Canada, select additional named *Gryllus* species found in Mexico and the Bahamas, plus the European field cricket *G. campestris* Linnaeus and the Afro-Eurasian cricket *G. bimaculatus* De Geer. *Acheta*, *Teleogryllus*, and *Nigrogryllus* were used as outgroups. Anchored hybrid enrichment was used to generate 492,531 base pairs of DNA sequence from 563 loci. RAxML analysis of concatenated sequence data and Astral analysis of gene trees gave broadly congruent results, especially for older branches and overall tree structure. The North American *Gryllus* are monophyletic with respect to the two Old World taxa; certain sub-groups show rapid recent divergence. This is the first Anchored Hybrid Enrichment study of an insect group done for closely related species within a single genus, and the results illustrate the challenges of reconstructing the evolutionary history of young rapidly diverged taxa when both incomplete lineage sorting and probable hybridization are at play. Because *Gryllus* field crickets have been used extensively as a model system in evolutionary ecology, behavior, neuro-physiology, speciation, and life-history and life-cycle evolution, these results will help inform, interpret, and guide future research in these areas.

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## Identification of specific DNA markers for two isolated populations of the desert locust, *Schistocerca gregaria* (Orthoptera: Acrididae)

Jamal, ZA; El-Deeb, N; Ghareeb, A; Ibrahim, HAM. 2020

Genomic DNA from two isolated gregarious locust populations in Africa had been amplified by using short decamer primers of random sequences. To identify markers that may distinguish between two major locust populations, northern *Schistocerca gregaria gregaria*, and southern *Schistocerca gregaria flaviventris*, 20 operon kit (A) primers from both populations were investigated with genomic DNA. Four primers generated low molecular weight polymorphic patterns. The primer (A2) showed a particular DNA amplified band (similar to 600 bp) from the southern *S. g. flaviventris* that was not expressed in the northern *S. g. gregaria*. For further examination, southern blot hybridisation indicated that this sequence is extremely repeated in the genome of the *S. g. flaviventris* population but not to the northern population. Therefore, this sequence may be highly specific to the southern locusts. Also, the southern population may constitute an evolutionary dichotomy that occurred on the African continent and can separate the populations of the two locusts into two distinct species.

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## The mosaic distribution pattern of two sister bush-cricket species and the possible role of reproductive interference

Dorkova, M; Kristin, A; Jarcuska, B; Kanuch, P. 2020

Reproductive interference can shape regional distribution patterns in closely related species, if prezygotic isolation barriers are weak. The study of such interaction could be more challenging in nuptial gift-giving species due to the direct nutritional effects on both sexes of both species during copulation. We mapped the distribution of two sister bush-cricket species, *Pholidoptera aptera* and *Pholidoptera transsylvanica*, at the northern margin of their overlapping ranges in Europe, and with a behavioral experiment, we tested the possibility of heterospecific mating. We found a very rare coexistence of species locally (0.5%, n = 391 sites) with mostly mutually exclusive distribution patterns, resulting in a mosaic pattern of sympatry, whereas they occupied the same climate niche in forest-dominated mountain landscape. Over 14 days of a mating experiment with seven mixed groups of conspecifics and heterospecifics (n = 56 individuals in total), the number of received spermatophores per female was 3-6 in *P. aptera* and 1-7 in *P. transsylvanica*. In total, we found 8.1% of heterospecific copulations (n = 99 transferred spermatophores with genetic identification of the donor species), while we also confirmed successful transfer of heterospecific sperms into a female's reproductive system. Because bush-cricket females also obtain required nutrition from a heterospecific spermatophylax what should increase their fitness and fecundity, we suggest that their flexibility to mate with heterospecifics is beneficial and drives reproductive interference. This may substantially limit the reproductive success of the less frequent species (*P. transsylvanica*), coupled with eventual detrimental effects from hybridization, and result in the competitive exclusion of that species from their areas of coexistence.

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## Genomic footprints of an old affair: Single nucleotide polymorphism data reveal historical hybridization and the subsequent evolution of reproductive barriers in two recently diverged grasshoppers with partly overlapping distributions

Tonzo, V; Papadopoulou, A; Ortego, J. 2020

Secondary contact in close relatives can result in hybridization and the admixture of previously isolated gene pools. However, after an initial period of hybridization, reproductive isolation can evolve through different processes and lead to the interruption of gene flow and the completion of the speciation process. *Omocestus minutissimus* and *O. uhagonii* are two closely related grasshoppers with partially overlapping distributions in the Central System mountains of the Iberian Peninsula. To analyse spatial patterns of historical and/or contemporary hybridization between these two taxa and understand how species boundaries are maintained in the region of secondary contact, we sampled sympatric and allopatric populations of the two species and obtained genome-wide single nucleotide polymorphism data using a restriction site-associated DNA sequencing approach. We used Bayesian clustering analyses to test the hypothesis of contemporary hybridization in sympatric populations and employed a suite of phylogenomic approaches and a coalescent-based simulation framework to evaluate alternative hypothetical scenarios of interspecific gene flow. Our analyses rejected the hypothesis of contemporary hybridization but revealed past introgression in the area where the distributions of the two species overlap. Overall, these results point to a scenario of historical gene flow after secondary contact followed by the evolution of reproductive isolation that currently prevents hybridization among sympatric populations.

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## Historical isolation facilitates species radiation by sexual selection: Insights from *Chorthippus* grasshoppers

Nolen, ZJ; Yildirim, B; Irisarri, I; Liu, SL; Crego, CG; Amby, DB; Mayer, F; Gilbert, MTP; Pereira, RJ. 2020



Theoretical and empirical studies have shown that species radiations are facilitated when a trait under divergent natural selection is also involved in sexual selection. It is yet unclear how quick and effective radiations are where assortative mating is unrelated to the ecological environment and primarily results from sexual selection. We address this question using sympatric grasshopper species of the genus *Chorthippus*, which have evolved strong behavioural isolation while lacking noticeable ecomorphological divergence. Mitochondrial genomes suggest that the radiation is relatively recent, dating to the mid-Pleistocene, which leads to extensive incomplete lineage sorting throughout the mitochondrial and nuclear genomes. Nuclear data shows that hybrids are absent in sympatric localities but that all species have experienced gene flow, confirming that reproductive isolation is strong but remains incomplete. Demographic modelling is most consistent with a long period of geographic isolation, followed by secondary contact and extensive introgression. Such initial periods of geographic isolation might facilitate the association between male signaling and female preference, permitting the coexistence of sympatric species that are genetically, morphologically, and ecologically similar, but otherwise behave mostly as good biological species.

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#### **Rhizobacterial treatment of bermudagrass increases tolerance to damage from tawny mole crickets (*Neoscapteriscus vicinus* Scudder)**

Coy, RM; Held, DW; Kloepper, JW. 2020

**BACKGROUND** Inoculation of bermudagrass with rhizobacterial biostimulants can increase plant growth and influence relationships with grass-feeding herbivores. Tunneling and root-feeding behaviors of tawny mole crickets cause severe damage to grass in pastures, golf courses, and lawns. The goal of this study was to determine if inoculation of bermudagrass by a rhizobacteria blend (plant growth-promoting rhizobacteria, PGPR) increases the tolerance of hybrid bermudagrass to tawny mole crickets in captivity and under field conditions. **RESULTS** Bermudagrass in arenas treated with a rhizobacteria blend then infested with tawny mole crickets produced significantly greater root lengths compared to bermudagrass that was either fertilized and infested with mole crickets, or bermudagrass without mole crickets. Bermudagrass treated with either the rhizobacteria blend or fertilizer produce similar top growth, and both treatments in the presence of mole crickets produced greater top growth than bermudagrass without mole crickets. Bermudagrass field plots infested naturally with mole crickets and treated twice with the rhizobacteria blend, or the rhizobacteria blend mixed with bifenthrin produced similar damage ratings as plots treated twice with bifenthrin. The rhizobacteria blend mixed with bifenthrin provided more consistent reductions in the surface activity of mole crickets relative to non-treated plots. **CONCLUSION** Enhanced growth of bermudagrass from fertilizer or rhizobacteria increased tolerance of bermudagrass to damage from tawny mole crickets. Application of PGPR or a PGPR-bifenthrin mixture to turfgrass damaged by mole crickets provided comparable reductions to a short residual, synthetic pyrethroid insecticide. Rhizobacterial products have potential utility for IPM of root herbivores. (c) 2019 Society of Chemical Industry

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#### **A revision of the shield-back katydid genus *Neduba* (Orthoptera: Tettigoniidae: Tettigoniinae: Nedubini)**

Cole, JA; Weissman, DB; Lightfoot, DC; Ueshima, N; Warchalowska-Sliwa, E; Maryanska-Nadachowska, A; Chatfield-Taylor, W. 2021

The Nearctic shield-back katydid genus *Neduba* is revised. Species boundaries were demarcated by molecular phylogenetic analysis, morphology, quantitative analysis of calling songs, and karyotypes. Nine previously described species are redescribed: *N. carinata*, *N. castanea*, *N. convexa*, *N. diabolica*, *N. extincta*, *N. macneilli*, *N. propsti*, *N. sierranus*, and *N. steindachneri*, and twelve new species are described: *N. ambagiosa* sp. n., *N. arborea* sp. n., *N. cascadia* sp. n., *N. duplocantans* sp. n., *N. inversa* sp. n., *N. longiplutea* sp. n., *N. lucubrata* sp. n., *N. oblongata* sp. n., *N. prorocantans* sp. n., *N. radicata* sp. n., *N. radocantans* sp. n., and *N. sequoia* sp. n. We chose a lectotype for *N. steindachneri* and transferred *N. picturata* from a junior synonym of *N. diabolica* to a junior synonym of *N. steindachneri*. Diversification in this relict group reflects cycles of allopatric isolation and secondary contact amidst the tumultuous, evolving geography of western North America. The taxonomy and phylogenies presented in this revision lay the groundwork for studies of speciation, biogeography, hybrid zones, and behavioral evolution. Given that one *Neduba* species is already extinct from human environmental disturbance, we suggest conservation priorities for the genus.

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#### **Land use and terrestrial arthropods at the Colombian Pacific coast**

Lohr, B; Narvaez, A. 2021

Diversity, permanence, and activity of terrestrial arthropods were investigated in four areas of different land use in the lowlands of the Pacific coast of Colombia with the aim to identify potential predator species for the palm root borer, *Sagalassa valida*. Ten pitfall traps were established along a 100 m transect in four areas: a secondary forest, a 20 year.-old peach palm plantation, and two hybrid oil palm plantations of three and seven years of age, respectively. Twenty-two collections were made covering a whole year. All ants were identified to species or morphospecies level, the other arthropods to order or where possible to family level. In total, 50,603 arthropods were captured, the most abundant were ants (37.0 %), followed by Collembola (35.4 %), Acari (10.6 %), Coleoptera (7.0 %) and Diptera, Hemiptera and Araneae in almost equal numbers (around 2.5 %). Orthoptera (92 % Gryllidae) were present in all collections, always at low numbers. The highest number of ants were recorded in the oil palm transects; Diptera, Hemiptera and Orthoptera were more numerous in the secondary forest, Acari, Araneae and Collembola in the palm transects. *Ectatomma ruidum* was by far the dominant ant species (84.9 % of all specimens) and absent from only 20 of the 880 captures. The second most frequent ant genus were army ants with two species, *Labidus praedator* and *L. coecus*. Rainfall, even area-wide flooding, and temperature did not explain variability in captures of any taxonomic group satisfactorily. We conclude that *E. ruidum* might be the predator to provide control of the root borer and recommend further studies on its efficiency.

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#### **Stable inversion clines in a grasshopper species group despite complex geographical history**

Guzman, NV; Kempainen, P; Monti, D; Castillo, ERD; Rodriguez, MS; Sanchez-Restrepo, AF; Cigliano, MM; Confalonieri, VA. 2022

Chromosomal inversions are known to play roles in adaptation and differentiation in many species. They involve clusters of correlated genes (i.e., loci in linkage disequilibrium, LD) possibly associated with environmental variables. The grasshopper "species complex" *Trimerotropis pallidipennis* comprises several genetic lineages distributed from North to South America in arid and semi-arid high-altitude environments. The southernmost lineage, *Trimerotropis* sp., segregates for four to seven putative inversions that display clinal variation, possibly through adaptation to temperate environments. We analysed chromosomal, mitochondrial and genome-wide single nucleotide polymorphism data in 19 *Trimerotropis* sp. populations mainly distributed along two altitudinal gradients (MS and Ju). Populations across Argentina comprise two main chromosomally and genetically differentiated lineages: one distributed across the southernmost border of the "Andes Centrales," adding evidence for a differentiation hotspot in this area; and the other widely distributed in Argentina. Within the latter, network analytical approaches to LD found three clusters of correlated loci (LD-clusters), with inversion karyotypes explaining >79% of the genetic variation. Outlier loci associated with environmental variables mapped to two of these LD-clusters. Furthermore, despite the complex geographical history indicated by population genetic analyses, the clines in inversion karyotypes have remained stable for more than 20 generations, implicating their role in adaptation and differentiation within this lineage. We hypothesize that these clines could be the consequence of a coupling between extrinsic postzygotic barriers and spatially varying selection along environmental gradients resulting in a hybrid zone. These results provide a framework for future investigations about candidate genes implicated in rapid adaptation to new environments.

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#### **The mechanical forces in katydid sound production**

Xiao, HP; Chiu, CW; Zhou, Y; He, XL; Epstein, B; Liang, H. NA

Katydid and crickets generate their characteristic calling sound by rubbing their wings together. The mechanisms of the rubbing force, however, have not been extensively studied. The change of mechanical force with external parameters (speed and applied load) in the stridulation process has not been reported. Our current study aims to investigate the mechanical forces of katydid stridulation. Four pairs of files and plectrums from a katydid, which are responsible for the katydid's sound production, were examined with a specially designed experimental configuration. Due to the asymmetric nature of the wing motion in their opening and closing, the contact between the plectrum and file resembles that of a ratchet. Multiple frequencies were generated during experimental wing rubbing so that a calling-like sound was produced. Results showed that the morphology of the plectrum/file contact has significant effects on mechanical forces induced on the wings and resulting sound production. The roles of the mechanical forces include sound generation, tone modification, and energy consumption. The findings in this work reveal the variation trend of mechanical force with sliding speed and applied load. The frequency and amplitude of the sound wave produced in tribo-test are close to those in natural condition. By mimicking the microstructure of the plectrum and file teeth, acoustic instruments with high mechanical energy conversion rate can be developed. Our results provide new approaches in the design and improvement of micro-machines for acoustic applications, as well as in hybrid robotic systems. (C) 2013 AIP Publishing LLC.

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