

REVIEW OF REPRODUCTIVE ISOLATING BARRIERS IN ODONATA

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Premating reproductive isolating barriers in Odonata involve temporal, habitat, and ethological barriers to interspecific gene exchange. Differences in visual and tactile stimuli comprise the most important and effective barriers within the order. Mechanical isolation, in the classical sense of incompatible genitalia, has not been demonstrated. Separation of potential mates during tandem (nongenitalic union) has been interpreted in some groups as a type of mechanical isolation. Postmating barriers have not been researched, although several hybrid dragonflies have been reported.

Speculation on isolating barriers far outweighs actual data. Studies are needed on the importance of tactile stimuli in Anisoptera and on the existence of mechanical isolation in both the genitalic and nongenitalic sense. Groups in which ethological isolation is expected but for which experimental studies do not exist are Gomphidae, Aeshnidae, Macromiidae, Corduliidae, Polythoridae, Megapodagrionidae, Pseudostigmatidae, Platystictidae, and Protoneuridae. The exact functions of the various structures used in mating still need to be clarified.

INTRODUCTION

The essence of the biological species concept, that groups of interbreeding populations are reproductively isolated from other such groups (MAYR 1970), prompts a fundamental question: how is interbreeding between species prevented? The term isolating mechanism was devised by DOBZHANSKY (1937) to encompass the ways by which interspecific gene exchange is prevented; the more current term, reproductive isolating barriers (RIBs) is used in this paper because it does not imply an evolved function as does the term mechanism. Knowledge of the exact barriers isolating the majority of closely related species of animals does not exist. Difficulties in understanding animal communication, especially in insects, have hampered isolation studies; a major stumbling block has been how iso-

lating barriers arise (modes of speciation) and the relative roles of natural selection and chance in these processes.

Given the advanced taxonomic status of the Odonata, their relatively large size and ease of recognition in the field, a fair knowledge of RIBs in dragonflies would be expected. Despite considerable information on reproductive behavior, and JOHNSON's review (1962) of reproductive isolation in which he pointed out areas where research was needed, there are large gaps in knowledge of the group. The purposes of this review are to briefly summarize present knowledge on odonate RIBs, to identify areas where study is needed, and to give some guidelines in approaching the study of RIBs in dragonflies.

STATE OF KNOWLEDGE

All published studies I reviewed were concerned with premating RIBs. Almost nothing is known of possible postmating mechanisms in Odonata, probably because dragonflies are difficult to hold captive and will not readily mate when confined. JOHNSON's techniques (1965) show promise that at least some damselflies may be cultured. The study of postmating RIBs could be especially rewarding in groups where interspecific tandem attempts frequently occur, as crosses are possible. JOHNSON (1975) reported 100 percent mortality of larvae hatching from eggs produced by interspecific copulations between *Ischnura damula* and *I. demorsa*, the only example of hybrid mortality yet known in Odonata. WAAGE (1975) assumed postmating barriers to be operative based on his observations of interspecific copulations and the absence of obvious hybrids between two species of *Calopteryx*. Discoveries of possible hybrid specimens (Table I) further point to the need for studies in this area.

PREMATING ISOLATING BARRIERS

The dominance of vision among the senses of dragonflies indicates its potential importance as a means of recognizing conspecific mates, and indeed this appears to be operative. On the other hand, barriers in addition to optical stimuli are also operating, as recognised by JOHNSON (1962). In the following discussion of the types of RIBs, the examples given are not intended as a complete compilation of the literature, but rather are used to show how the RIBs operate.

Table I

A list of dragonfly species reported to have produced hybrid individuals (main sources: Kiauta 1967; Asahina 1974)

GOMPHIDAE					
<i>Gomphus fraternus</i>	X	<i>G. externus</i>	♀	Calvert	1901
<i>Gomphus lividus</i>	X	<i>G. grasilinellus</i>	♂	Williamson	1903
AESHNIDAE					
<i>Aeshna confusa</i>	X	<i>A. diffinis</i>	♂	Calvert	1956
<i>Anax imperator</i>	X	<i>A. parthenope</i>	♂	Bilek	1955
<i>Anax nigrofasciatus</i>	X	<i>A. parthenope julius</i>	♂♂	Hiura	1968
<i>Anax nigrofasciatus</i>	X	<i>A. parthenope julius</i>	♀♀	Hiura	1971
<i>Anax nigrofasciatus</i>	X	<i>A. parthenope julius</i>	♂♂	Asahina	1974
LIBELLULIDAE					
<i>Leucorrhinia glacialis</i>	X	<i>L. intacta</i>	♂	Tennessen	1981
<i>Libellula pulchella</i>	X	<i>L. luctuosa</i>	larva	Wilson	1920
<i>Sympetrum pedemontanum elatum</i>	X	<i>S.e. eroticum</i>	♂♂♀	Asahina	1974
<i>Sympetrum pedemontanum elatum</i>	X	<i>S.e. eroticum</i>	♀	Miyazaki	1972
<i>Sympetrum baccha matutinum</i>	X	<i>S.e. eroticum</i>	♂	Yamamoto	1965
<i>Sympetrum risi risi</i>	X	<i>S.e. eroticum</i>	5 ♂♂♀	Asahina	1974
COENAGRIONIDAE					
<i>Coenagrion pulchellum</i>	X	<i>C. puella</i>	♂	Bilek	1963
<i>Enallagma civile</i>	X	<i>E. carunculatum</i>	♂♂	Williamson	1906
SUMMARY: 12 different species pairs involved, 24+ specimens.					

Temporal isolation.

The two modes of temporal isolation, i.e. differences in flight season and diel reproductive periods, involve nonoverlap in the time of adult mating readiness. Obviously the absence of a species during the mating activity of a related species would effectively prevent interbreeding. However, few cases have been documented in Odonata.

An example of seasonal isolation may exist in the North American genus *Gomphaeschna*, wherein adults of *G. furcillata* appear earlier than those of *G. antilope* (GLOYD 1940). Although flight seasons overlap where they are sympatric, *G. antilope* adults do not appear to be reproductively mature before adults of *G. furcillata* disappear (unpublished observations). The literature is replete with seasonal differences between species, although relevance to reproductive isolation has been ignored. Data on relative abundance through time and on reproductive maturation, including frequencies of conspecific and heterospecific encounters, are needed. Until such studies are carried out, the importance of season in Odonata repro-

ductive isolation remains unknown.

On a diel basis, an example of temporal isolation between two species of Corduliidae was offered by PAULSON (1973). The coenagrionid *Enallagma dubium* appears to be partly isolated from its congeners by mating earlier in the day (TENNESSEN 1975), although two females were observed being taken into tandem by males of *E. pollutum*. MAY (1980) reported differences in the daily activity periods of four species of *Micrathyria*, although much overlap occurred and exact mating times were not given. MIZUTA's study (1974) showed distinct temporal differences in three damselflies, but the species were not congeneric and the isolation appeared to be a response to predation pressures on the smaller species.

Temporal isolation is probably not widespread in Odonata, perhaps because it is relatively inefficient. Variation amongst individuals and environmental changes lead to overlap in breeding times, in which case another barrier would be necessary. Temporal differences in mating appear to function secondarily as RIBs in some groups, but probably have not evolved directly as such (PAULSON 1973).

Habitat isolation

Often referred to as ecological or microgeographic isolation, habitat isolation involves differences in the microhabitats where copulation of sympatric species is initiated; in terms of distance, these differences may be exceedingly small. Adults of related species may be present simultaneously during certain activities, such as mixed swarm-feeding (CORBET 1963), but mating may occur in different types of habitat. Conversely, even though larvae may live in distinctly separate microhabitats, adult behavior may obliterate the difference.

Isolation due to habitat differences results from adult behavior, recognition of which prompted GARRISON (1979) to classify it as an ethological barrier. However, because habitat isolation does not involve differences in behavior during encounters between heterospecific males and females, it represents a special case (i.e. isolation is effected via specific responses to extrinsic stimuli), and is therefore placed in a distinct category.

Groups in which evidence of habitat isolation has been found include *Enallagma* (TENNESSEN 1975, GARRISON 1979), *Progomphus* (BYERS 1939), *Tetragoneuria* (TENNESSEN 1977), *Ischnura* (JOHNSON 1966, VERDONK 1979), *Leucorrhinia* (PAJUNEN 1962), *Somatochlora* (TAKETO 1960). In these examples, habitat isolation is an inefficient barrier, as the potential for individuals to

transgress habitat "boundaries" is great, making likely interspecific encounters. The experimental results of JOHNSON (1966) strongly suggest that habitat changes could cause a breakdown of segregation. This breakdown necessitates the presence of another RIB.

Ethological isolation

Several examples of ethological or behavioral isolation have been elucidated. In these barriers, heterospecific individuals (potential mates) meet but mating is prevented by intrinsic differences in the acts that elicit the copulatory response. There are four basic means (based on the senses) by which species "recognition" can be achieved.

- (1) *Visual stimuli.* A wide variety of visual stimuli have been found to evoke the mating response in dragonflies, and others are bound to be discovered. Courtship has been described in four Zygopteran families: Calopterygidae (BUCHHOLTZ 1951, 1955; JOHNSON 1961; HEYMER 1973; WAAGE 1973), Chlorocyphidae (CORBET 1963; CONSIGLIO 1974), Platycnemididae (BUCHHOLTZ 1956; HEYMER 1966), and Hemiphlebiidae (TILLYARD 1913). Color patterns and ways in which they are displayed to the female are critical in pair-forming in many of these groups, but only one study has focused on their role in reproductive isolation (WAAGE 1975).

Studies on Libellulidae have shown that courtship and sexual dimorphism are important in sex "recognition" and the acquisition of a mate (JACOBS 1955; ITO 1960; PARR & PARR 1974). However, I am aware of only one study demonstrating visual isolation in this large, diverse family (PAJUNEN 1964). He concluded that males of two similarly colored *Leucorrhinia* species recognize females by differences in abdominal size, and females appear to recognize males by undetermined sight stimuli prior to tandem attempts. Numerous other libellulid genera come to mind in which striking color and color-pattern differences exist amongst the species (*Celithemis*, *Erythrodiplax*, *Libellula*, *Micrathyria*, *Rhyothemis*), but they have not been studied.

JOHNSON (1975) proposed that male-like andromorphs within *Ischnura* offer increased reproductive isolation, as he found male mating preferences in two

species. However, GARRISON (1979) did not detect morph preferences by males in two *Enallagma* species. Many groups contain polymorphic species for study of this possible barrier. Other visual cues, such as differences in flight behavior and form discrimination, are likely to be discovered. Distinctive patterns of ultraviolet reflections have been found in several species (SILBERGLIED 1979), and UV receptors have been found in compound eyes and ocelli (MENZEL 1979). The need for experimental work on these various possible modes of visual isolation is obvious.

- (2) *Tactile stimuli.* Experimental evidence that tactile stimuli function as RIBs was first presented by LOIBL (1958) and KRIEGER & KRIEGER-LOIBL (1958). Females of *Lestes* and *Ischnura* refused to copulate with males having experimentally altered appendages. TENNESSEN (1975) concluded that tactile stimuli provided by the male superior appendages release copulatory behavior in females of two species of *Enallagma* and that specific differences in the shape of these appendages appear to be isolating the species. ROBERTSON & PATTERSON (1982), using an experimental approach with *Enallagma*, found strong evidence of tactile recognition of males by females based on superior appendage shape.

These examples of tactile isolation differ in one basic respect from the tactile mechanism described in other groups of insects. In studies of other insects, tactile stimuli consist of males "using" a particular organ in a specific manner, even though the shape of the organ may be similar in the species under study (BARTH 1968; DOBZHANSKY 1970). The differences arise from the behavior, which evokes acceptance or rejection by the female. Tactile stimuli in some groups are just one step in a series of signals exchanged between potential mates. In the Odonata studied thus far, however, the differences appear to arise from the shape of the contacting organ(s), which is detected and discriminated by females. This hypothesis involves behavior and merits classification as an ethological barrier. Tactile isolation appears to be very effective, and in some odonates may serve as the ultimate premating RIB should other de-

vices break down.

- (3) *Olfactory* and (4) *Auditory stimuli*. Neither chemical substances nor sound waves have been implicated as communicative signals in Odonata, although research effort in these areas is almost nil. Recognition of the visual acuteness of dragonflies has obviously dominated approaches to the study of their biology. And although long-range chemoreception seems unlikely, the possibility of contact chemoreception deserves attention. The fact that males attempt tandem when presented females that have been dead for days or even weeks (any pheromone would have dissipated) does not rule out chemoreception as males may be producing the chemical and females detecting it. WILLIAMSON (1906) reported a white substance left on the female mesostigmal plates by males of several species of *Argia*. He postulated that the material may function in strengthening the tandem bond. Is this a common phenomenon and could the material be dried, displaced seminal fluid, or could it contain a pheromone? Cells that appear to be secretory were found in the superior appendages of *Enallagma* males (TENNESSEN 1975) but their function has not been determined. Experimental procedures for solving these problems are not easily devised, and other approaches, such as chemical analysis, may be rewarding. To my knowledge, the possibility of sound detection in dragonflies has not been thoroughly investigated.

In summary, ethological isolating barriers may effectively prevent interspecific gene exchange, as there are few reports of copulation between closely related species thought to be ethologically isolated (see BICK & BICK 1981). The majority of cognate species of Odonata may be isolated by ethological means, with visual and tactile differences playing the major roles.

Mechanical isolation

Also called the "lock-and-key" hypothesis, this idea has come under much criticism, as few supposed examples in the Insecta have withstood scrutiny. Incompatibility of genitalia has not been demonstrated convincingly in any odonate species. WATSON (1966) speculated that in *Tramea* male hamules interlock with the female genitalia; JOHNSON's study (1972) showed that these structures in *Hagenius*

probably support the penis during sperm translocation, casting doubt on a lock and key operation. More work is needed in Anisoptera on how the genitalia are engaged and held together (i.e. how do hamules function?). Another mechanical barrier which has been proposed is incompatibility in tandem linkage, the nongenitalic union preceding copulation (i.e. inability of males to securely clasp females with anal appendages because of anatomical differences). JOHNSON (1962) and CORBET (1963) cited several studies considered to provide evidence of this type of isolation. PAULSON (1974) presented experimental evidence from several coenagrionid genera that he considered supportive of the hypothesis. Based on my own observations and understanding of other studies, I believe that what has been interpreted as mechanical isolation may involve tactile stimuli. Females of two *Enallagma* species, upon being taken into tandem by heterospecific males, performed "refusal motions" and were released (TENNESSEN 1975). When presented dead heterospecific females, males had no difficulty in securely clasping them. PAULSON interpreted "difficulties associated with the fitting of the male appendages to the female thorax" as mechanical isolation. However, the "difficulty" could arise from female discrimination based on inappropriate stimuli from a heterospecific male. Separation of such pairs gives the appearance of a mechanical barrier when contact stimuli and behavior are involved.

A different type of mechanical isolation may be hypothesized using WAAGE's discovery (1979a) that males remove sperm stored in the female's bursa copulatrix from previous matings. The barrier would work as follows: a female of species A mates with a male of sp. A, but before oviposition, she is taken into tandem by a male of sp. B; barring any other type of isolation, copulation is attempted; however, the intromittent organ is not of the correct shape or length to remove sperm of the sp. A male; no sperm from the sp. B male are transferred. The hypothesis would not apply if a male does not have to remove the previous male's sperm in order to transfer his own because sperm of the last male to mate appear to have precedence in fertilizing eggs (see WAAGE 1979a for discussion and references). The hypothesis also would not hold for those species ovipositing in tandem following copulation. If this hypothesis is correct for at least some species pairs, it would fit the classical definition of mechanical isolation in that genitalic incompatibility is involved. However, much of the morphology of the odonate penis probably evolved to facilitate sperm displacement (WAAGE 1982), and any resulting reproductive isolation may be only an occasional consequence.

BREAKDOWN AND REINFORCEMENT

The above premating RIBs are probably not 100% effective, and how interspecific gene exchange is prevented should supposed barriers fail is unknown. Nevertheless, RIBs have been viewed as operating in sequence, or series, one reinforcing another. Accordingly, temporal or habitat differences may isolate two sympatric species for the most part; if heterospecific individuals meet, they may "recognize" differences visually and avoid mating. If visual stimuli are absent or inefficient, a tactile or mechanical RIB may intervene. Failure of these barriers would result in interspecific mating, in which case post-mating RIBs, such as chromosome incompatibility (no fertilization), zygote or hybrid mortality, sterility or inferiority may prevent hybridization. Interspecific mating is apparently a rare phenomenon in Odonata (BICK & BICK 1981).

With each step in the foregoing sequence, there appears to be an increase in wastage of time and energy devoted to securing a conspecific mate. For example, selection would seem to favor those males that visually discriminate against heterospecific females versus those that attempt to mate with any female. However, owing to different sexual selection pressures in different groups, females may or may not be distinguishable. Nondescript females are furtive near breeding sites, and in these groups it may be more advantageous for males to attempt tandem with any female, thereby increasing the chance of obtaining a mate. Problems such as this stem from unanswered questions concerning how RIBs originate (i.e. how do organisms speciate?). Although it has been postulated that isolating barriers arise or are perfected via natural selection after incipient species come into contact (MAYR 1970, BUSH 1975, WHITE 1978), very little supportive evidence has been found (PATERSON 1978). It is possible that many barriers to gene exchange are incidental or pleiotropic consequences of other evolved functions (ROBERTSON & PATERSON, 1982. Further advancement of speciation theory may benefit from population-genetic studies of isolating barriers (TEMPLETON 1981).

CONTINUING THE QUEST — STUDY NEEDS

The biggest gap in our knowledge of RIBs in Odonata concerns the importance and effectiveness of ethological barriers in the large anisopteran families Aeshnidae, Gomphidae and Corduliidae; studies are also needed on Cordulegasteridae, Macromiidae and Synthemist-

idae. Observations on mating behavior of closely-related species in these groups are scanty, and experimental data are nonexistent. Rarely has the entire mating sequence for any species within these groups been observed, due to the unknown whereabouts of the sexes prior to meeting, their rapid flight, and disappearance from the site once tandem is achieved. However, a number of tandem pairs involving heterospecific individuals have been collected (BICK & BICK 1981). In general, these species belong to groups in which the wings are hyaline and courtship behavior is unknown, evidence that visual stimuli are nonexistent or unreliable, and that isolation is effected once contact is made. Male appendages in a large number of aeshnids, gomphids and corduliids are uniquely shaped, indicating that tactile and/or mechanical differences might be the effective barriers. Male appendages of cordulegasterids and macromiids are remarkably uniform amongst the species, much as in libellulid genera, and discovering the RIBs in these groups is especially challenging. Much more study of Libellulidae is needed.

Very little has been published on behavior and isolation of neotropical Zygoptera, in which many unusual structural and color differences exist between related species. Intriguing problems and discoveries await investigators who undertake studies of Polythoridae, Megapodagrionidae, Pseudostigmatidae, Platystictidae and Protoneuridae, as well as the Chlorocyphidae and Epallagidae of other parts of the world. There are large genera in the Coenagrionidae, such as *Acanthagrion*, *Argia* and *Ischnura* for which very little behavioral knowledge is available. Much remains to be learned in the Calopterygidae.

The terms used by various workers for behavioral acts and morphological structures are not uniform (BICK 1972) and effort should be directed toward a terminology that will prevent confusion and minimize interpretive difficulties. Research is needed to document and clarify the difference between tactile and mechanical isolation, and in defining the importance of each barrier in certain groups. Female polymorphism and sperm removal are two possible barriers requiring further study. The possibility of contact chemoreception in Zygoptera deserves attention. No published work on postmating barriers has appeared, although studies are being conducted by Dr. S. Obana and Mr. T. Takeuchi on *Sympetrum* in Japan (K. Inoue, pers. comm.).

The exact functions of the different structures comprising the male accessory genitalia and how they are used in mating are still in need of clarification. There is a large degree of variation in the structure of these parts within the order, and different functional roles

for homologous structures may exist. Studies by PFAU (1971), JOHNSON (1972), and WAAGE (1979a, 1982) have furthered understanding of the sperm-transfer process. Such research may uncover mechanical isolating barriers. Difficulties arise from having to reconstruct relationships of male and female parts, as direct observations during copulation is rarely possible, and rarely do pairs stay in the wheel position after being collected.

PROBLEM-SOLVING GUIDELINES

Temporal and ecological isolation should be investigated initially to determine the extent of isolation afforded by either in the group under study. Population changes through time, maturation periods, mating frequencies and movement must be considered. Marking techniques and analyses, such as described by GARRISON (1978), are particularly useful. Any overlap between species in time or space indicates a potential for heterospecific males and females to meet, and other barriers must be sought.

In ethologically-isolated species, the use of models can answer such questions as (1) what aspects of the female elicit a tandem response in males? (2) do males visually discriminate between females of the different species? Models can be presented to males using the fishing-line technique (ST. QUENTIN 1934; MOORE 1952), or ventrally-supported technique (KRIEGER & KRIEGER-LOIBL 1958; PAULSON 1974; TENNESSEN 1975; WAAGE 1975). With the latter technique, there is nothing to interfere with a male's attempting to land on a model, so details of tandem behavior can be observed. If visual isolation is found lacking, a tactile or mechanical barrier can be presumed; differentiating the latter two can be problematical. Evidence in favor of tactile isolation includes: (1) females taken into tandem by heterospecific males do not cooperate and even though males are able to clasp them and fly in tandem, the females perform escape and/or refusal motions and tandem is broken; (2) when presented dead female models of different species, males are able to achieve tandem and securely hold them. Further experimental evidence can be obtained by altering the shape of the male appendages and observing their success in tandem attempts with conspecific females, although such techniques may be difficult to control. Evidence of a mechanical barrier would be: (1) separation of heterospecific pairs before secure tandem can be achieved (this could also result from some type of tactile requirement, however); (2) separation of the pair with a lack of refusal motions by the female; (3) a break in copulation without sperm transfer.

If interspecific copulation is observed, every attempt should be made to obtain eggs and rear larvae. Hybrids may result, although the possibility that the eggs were fertilized with sperm from a previous conspecific mating can not be ruled out. Therefore, attempts to artificially fertilize eggs with sperm from other species are needed, especially using species previously seen in interspecific copulation or tandem. The techniques used by FREMLING (1967) for mayflies may be applicable.

CONCLUDING REMARKS

- (1) Visual stimuli may be important barriers isolating species with distinctive color patterns, whereas tactile differences may be equally important in clear-winged or uniformly-colored groups; more work is needed in the understanding of mechanical isolation in Odonata.
- (2) Behavioral and morphological characteristics, some of which are important in isolating species, often vary amongst populations within the geographic range of species; research should focus on possible character displacement and the importance of selection in the origin of RIBs (WAAGE 1979b).
- (3) Knowledge from reproductive isolation studies should be used in efforts to solve difficult taxonomic problems; such application could serve as a test of conventional taxonomy.

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