International Journal of Odonatology 3 (2): 141-151, 2000

INTERSPECIFIC ENCOUNTERS BETWEEN MALE AESHNIDS DO THEY HAVE A FUNCTION?

Norman W. Moore
The Farm House, 117 Boxworth End, Swavesey,
Cambridge, CB4 5RA, United Kingdom

Received 04 April 2000; revised and accepted 01 August 2000.
Key words: Odonata, dragonfly, Aeshnidae; interspecific interactions; species recognition; aggression; practice

Abstract

Male aeshnid dragonflies at a small pond (circumference ca 90 m) in Cambridgeshire, U.K. generally pursued males of other aeshnid species as well as their own. As a result of these encounters the pursued insect frequently left the pond, particularly when it belonged to a smaller species. Libellulids, which differed greatly from the aeshnids in size and appearance, were also pursued. Male aeshnids attacking males of other species frequently pressed home their attacks even when they were close enough apparently to identify the pursued insect. Consequently interspecific pursuits appear to have a function over and above ensuring that no opportunity is lost to mate or to drive out a conspecific rival. It is suggested that a positive function of interspecific pursuit is practice in developing fighting skills against conspecifics.

Introduction

Interactions between males of different species of Odonata are common and have often been recorded. For a recent review see Corbet (1999: 450). Male aeshnids on their breeding waters may ignore males of other species but generally they respond to them. Responses range from mere inspection to pursuits of varying intensity, and even to physical fighting. Interactions between males of different species may leave both insects where they were before the encounter, or may result in the pursued insect leaving the water area. It is not at all clear what these interspecific interactions signify.

The pioneer work of Pajunen (1962, 1964, 1966) on *Leucorrhinia* species showed how varied interspecific responses could be in these libellulids and how difficult it was to interpret them. Drive and maturity of individual insects vary as do specific differences in methods of recognition (Frantsevich & Mokrushov, 1984). Interspecific encounters are a conspicuous feature of odonate behaviour yet little seems to have been published about their biological significance. Peters (1972) noted that *Anax parthenope* (Sélys) drives out most other aeshnids from its territory but itself is nearly always driven out by *Anax imperator* Leach. This led him to a discussion on whether the distributions of *A. parthenope* in Europe and of other aeshnid species in Mexico, Cuba, Europe and Asia were partly controlled by interspecific competition.

Singer (1987) suggested that the reason why *Leucorrhinia* males defend territories from heterospecific males as well as from conspecific ones is because "males cannot afford to hesitate when an intruder enters a territory, because any hesitation will reduce the probability of winning the ensuing conflict." Thus, while pursuing heterospecifics may have advantages over not pursuing them, the pursuit of heterospecifics may not have any other advantage.

The whole subject of interspecific interactions between male insects, and in particular Singer's hypothesis seemed worthy of more study. My pond at my home in Cambridgeshire, England (Moore 1987) provided an exceptional opportunity. Earlier observations (Moore 1964) on adult dragonflies by water-filled bomb holes in Dorset had shown that in so far as aeshnids were concerned each bomb hole could only support one adult male. Thus interspecific encounters between aeshnids in very small waterbodies always led to a clear-cut result, which indicated the dominance of one species over another. My pond in Cambridgeshire is much larger than a bomb hole and is large enough to support breeding populations of five species of aeshnids of different sizes: *A. imperator* (78 mm long), *Aeshna grandis* (Linnaeus) (73 mm), *Aeshna cyanea* (Müller) (70 mm), *Aeshna mixta* Latreille (63 mm) and *Brachytron pratense* (Müller) (55 mm). Measurements are from Hammond (1983). For *A. imperator, A. grandis* and *A. cyanea* my pond is too small to hold more than one male of each species. However, unlike the Dorset bomb holes it is large enough to support males of two or three different species at the same time. Thus many more interspecific interactions could be observed than on the bomb holes. Interactions could be recorded accurately because the whole pond could be kept under observation all the time from one place.

The objective of this study was to obtain as much information as possible about the frequency and outcome of the different encounters between adults of the five aeshnid species on the pond in order to throw light on the nature and possible function of the encounters.

Methods

The pond was dug at the end of 1983. It is pear shaped with the long axis running from east to west. It is ca 38 m long and ca 15 m wide at its widest part. The circumference is about 90 m. Emergent vegetation round its circumference consists mainly of *Typha latifolia* Linnaeus, *Phragmites australis* (Cav.) Trim. ex Steud., *Sparganium erectum* Linnaeus and *Iris pseudacorus* Linnaeus. Submerged vegetation consists largely of *Chara* spp. and *Callitriche* spp., *Nymphaea alba* Linnaeus and *Potamogeton natans* Linnaeus are the floating species. The pH of the water is just below neutral. The pond is surrounded by rough grassland and is backed by bushes and trees.

Eighteen species of Odonata have been recorded on the pond of which the following regularly complete generations: *Coenagrion puella* (Linnaeus), *Enallagma cyathigerum* (Charpentier), *Pyrrhosoma nymphula* Charpentier, *Ischnura elegans* (Vander Linden), *Lestes sponsa* (Hansemann), *B. pratense, A cyanea, A. grandis, A. mixta, A. imperator, Libellula depressa* Linnaeus, *Libellula quadrimaculata* Linnaeus, *Sympetrum sanguineum* (Müller) and *Sympetrum striolatum* (Charpentier). *Orthetrum cancellatum* (Linnaeus) occasionally breeds.

The observations in this paper were made in 1995, 1997, 1998 and 1999. The total amount of time making them was approximately 264 hours. I recorded all pursuits by one aeshnid of another. I obtained an index of the strength of each pursuit by recording whether or not the pursued insect was driven across the boundary between the water and the surrounding grassland. No distinction was made between occasions when the pursued insect returned shortly afterwards or much later. Supporting observations were made on occasions when two insects were within five metres of each other and merely investigated each other or ignored each other altogether, also on feeding patterns, the heights at which aeshnids patrolled and when they perched. Numerous but less complete records were kept on encounters between aeshnids and libellulids.

In this paper the word 'pursue' is used in its neutral sense of 'seek after' when describing one insect following another. It is not used in the sense of 'following with intent to capture or kill', since this begs the question of its function.

Results

Overlap of flying seasons

An indication of the overlap between the flying seasons of the five aeshnid species, and hence the opportunities to interact, is given in Fig. 1, which shows the situation in 1999, the year for which records were most numerous. There was some variation between the years. Most notably *A. imperator* and *A. mixta* did not overlap in 1995, 1997 and 1999 but did so in 1998. 1999 was the only year in which *B. pratense* was observed to overlap with another aeshnid species (*A. imperator*) and then only for one day. Therefore generalisations about aeshnids are largely based on observations made on the four other species. The differences in the overlap of the flying seasons of the different species and hence on the number of records of interactions which could be obtained account for the unevenness of the data below.

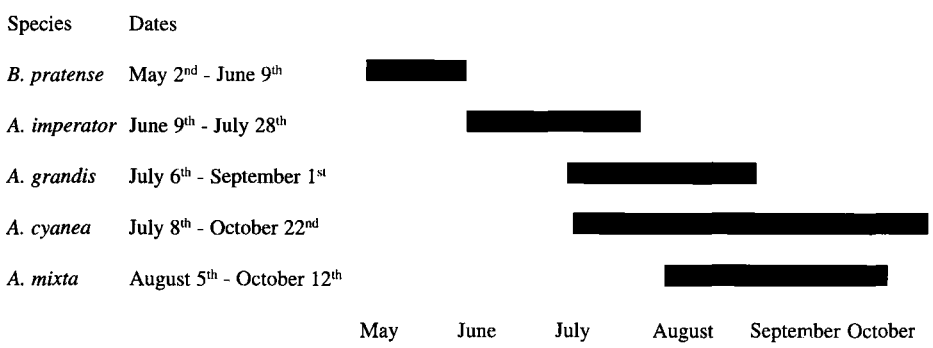

Figure 1. Flying seasons of aeshnid dragonflies at the Swavesey Pond 1999.

The relative frequency of conspecific and heterospecific pursuits

The numbers of *B. pratense* and *A. imperator* in the vicinity of the pond were too few for comparison to be made between their conspecific and heterospecific encounters. (See footnote on Table 1.) However, for the more numerous species whose conspecifics and heterospecifics were continually attempting to set up territories by the pond the total numbers of conspecific and heterospecific encounters observed give a rough indication of the relative frequency of the two types of pursuit in the circumstances provided by the Cambridgeshire pond. Table 1 shows that heterospecific pursuits by *A. grandis* and *A. cyanea* outnumbered conspecific pursuits by over three to one. The pond could hold two to three territories of *A. mixta* so it is not surprising that in this species conspecific pursuits outnumbered heterospecific ones. Heterospecific pursuits take up much of the time and hence energy of adult male aeshnids and clearly constitute a very significant activity.

Table 1. The frequency of conspecific and heterospecific pursuits during 264 hours of observation in 1995, 1997, 1998 and 1999 on the Swavesey pond.

Species	Number of conspecific pursuits	Number of heterospecific pursuits	Heterospecific pursuits / Conspecific pursuits
Aeshna grandis	83	289	3.48
Aeshna cyanea	106	370	3.49
Aeshna mixta	209	148	0.71

The numbers of *B. pratense* and *A. imperator* in the vicinity were very small, and for most of the time the territory holder belonging to these species was not challenged by a conspecific male: in the whole period of the observations no conspecific pursuits by *B. pratense* were observed and only three by *A. imperator*. For this reason records of *B. pratense* and *A. imperator* are not comparable with those of the other three species and are excluded from the table.

Eleven heterospecific pursuits by *B. pratense* and 202 by *A. imperator* were observed.

The outcome of conspecific and heterospecific pursuits

The outcome of interactions between male aeshnids are summarised in Table 2. In a pond as small as mine conspecific pursuits usually resulted in the pursued insect leaving the pond. On those occasions when it did not it was soon chased again and then left, with the result that the pond never contained more than one male each of the larger species for more than a very short time. When, as usually was the case, the insects could be followed closely the victor was almost invariably seen to be the territory holder. In conspecific encounters *A. mixta* males were usually pursued off the pond temporarily, but often the pursued insect returned to patrol in another part of the pond or it escaped the notice of the pursuer by returning and perching on emergent vegetation.

Table 2. Pursuits by male aeshnid dragonflies on the Swavesey pond and their outcome.

Pursuing species (Body length)	Number of pursuits (number of occasions pursued insect was driven from pond) Percentage of pursuits when pursued insect was driven from pond Pursued Species (Body length)				
	A. imperator 78 mm	*A. grandis* 73 mm	*A. cyanea* 70 mm	*A. mixta* 63 mm	*B. pratense* 55 mm
Anax imperator	**3(3)***	155(62)* +	20(20)*	7(5)	20(6)*
78 mm	100%	40%	100%	70%	30%
Aeshna grandis	175(4)	**83(71)***	49(23)*	65(39)*	
73 mm	2%	86%	47%	60%	
Aeshna cyanea	6(1)	107(46)*	**106(97)***	257(226)*	
70 mm	17%	43%	92%	88%	
Aeshna mixta	2(0)	55(9)	91(21)	**209(143)***	
63 mm	0%	16%	23%	68%	
Brachytron pratense	11(0)				
55 mm	0%				

Conspecific pursuits in bold.

* The pursued insect was attacked vigorously on one or more occasions.

\+ 49 of the pursuits of *A. grandis* by *A. imperator* were made by an old male *A. imperator* and did not cause the *A. grandis* to leave the pond. If these records are excluded, 58% not 40% of the pursuits of *A. grandis* by *A. imperator* resulted in *A. grandis* leaving the pond.

By contrast the outcomes of heterospecific interactions were much more varied. They ranged from ignoring the other species, merely investigating it, pursuing it with varying degrees of intensity to physical fighting. Unlike the situation between conspecifics the pursued male was often a territory holder.

On quite numerous occasions males of one species would appear to ignore males of other species, even when they flew quite close to them. This situation nearly always occurred when one of the insects was an *A. grandis*: on 51 occasions when records were kept of this behaviour, 48 involved *A. grandis*: on 22 of them another species ignored *A. grandis* and on 26 an *A. grandis* ignored the male of another species. *A. grandis* is markedly different in appearance from the other species on the pond. It is mainly brown with brownish wings, whereas the other species have bold patterns of blue or green and black or dark brown and clear wings. Similarly, when a male aeshnid was seen to investigate a male of another species and not pursue it one of the insects was nearly always an *A. grandis*.

When encounters resulted in pursuits, as they generally did, the outcome varied between species. The data in Table 2 indicate that the outcomes of pursuits were correlated with size of insect. *A. imperator*, much the largest species, was rarely driven from the pond by other species. Contrariwise the small *A. mixta* was usually driven

off by other species and rather rarely drove them off. The intermediate sized, similarly sized *A. grandis* and *A. cyanea* were evenly matched. Following heterospecific pursuits the pursued insect usually returned to the pond. Despite its small size *A. mixta* was frequently observed to be the first to attack males of larger species. The latter then turned on the *A. mixta* and pursued it vigorously. The reason for the anomalously few occasions when the very large *A. imperator* drove off the very small *B. pratense* is not clear. Conceivably *B. pratense* escaped pursuit because it patrols very close to the surface of the water.

Very vigorous, clearly aggressive pursuits were observed on occasion in all types of interaction (see Table 2) except for the following: no other species was ever seen to attack *A. imperator* very aggressively, and *A. mixta*, while sometimes it pursued *A. grandis* and *A. cyanea* from the pond, was never observed to attack them very aggressively, i.e. pursuing very closely or making physical contact.

Factors other than seasonal overlap and size of insect which affected the frequency and outcome of heterospecific pursuits

While the general nature of heterospecific interactions was clear from the observations, the number and outcome of some individual encounters were seen to be affected by specific differences in behaviour and the condition of individual insects.

As noted by Kaiser (1974) and others *A. cyanea* males only make quite short visits to water, and thus the species was often absent from the pond. By contrast *A. imperator* and *A. grandis* spent long periods patrolling without leaving or perching. Unlike these species *A. mixta* spent much time perching by water as well as patrolling. Since aeshnid males practically never attack perched males, *A. mixta* could spend much time by water without being pursued.

To a limited extent the number of interactions were reduced because the different species tended to fly at different heights. On its own *A. mixta* usually flew at a lower level than *A. grandis*, but when *A. grandis* was present *A. mixta* would often fly high above it.

An unexpected amount of feeding was observed to take place over water by all species, especially at the beginning and end of the day. Species varied when they came to water and left it. This affected the times they fed there. Whereas the larger species rarely appeared before 0900 solar time *A. mixta* often did and stayed later. For example on August 13th 1998 *A. mixta* was first seen at 0832 and last seen at 1721 solar time, whereas *A. cyanea* first appeared that day at 1010 and was last seen at 1552. These differences may have had some effects on encounters because it appeared that males sometimes did not pursue other males when they themselves were feeding.

Obvious differences in the condition of individual insects were seen to affect the outcome of interspecific encounters. An *A. imperator*, which from its battered appearance and flight appeared to be old, left the pond after being pursued several times by a very much smaller *A. mixta*. An *A. grandis*, similarly showing signs of age, was observed to pursue very few other aeshnid males. An *A. mixta* successfully drove from the pond an *A. cyanea* with a seriously damaged wing. Some individual insects appeared to be particularly aggressive: one *A. cyanea* kept the whole pond totally free of

other dragonflies (*A. cyanea, A. mixta* and *S. striolatum*) for 16 minutes. An immature *A. cyanea* was observed to patrol the marsh at the end of the pond not venturing to patrol the open water whether or not a mature *A. cyanea* was there.

Aeshnid males gave every indication of learning from experience. They clearly had good topographical memories. Several species quickly returned to a particular sunny, sheltered area once they had discovered it. Frequently an *A. mixta* would leave a favoured spot when a larger *A. cyanea* or *A. grandis* appeared, but when the larger insect left the *A. mixta* would return to it. An *A. grandis* was observed to avoid one end of the pond when an *A. cyanea* was there but returned to it when the *A. cyanea* left. As noted above *A. mixta* appeared to fly much higher when a larger species was present. These examples suggest that on occasions learning reduces the number of heterospecific interactions.

Interactions between aeshnids and libellulids

Aeshnids and libellulids were frequently observed to pursue each other. Sample records were made to determine which species were involved and to obtain an indication of the outcome of these interfamily pursuits. The data in Table 3 show that all species interacted with each other when their flying seasons overlapped. The encounters rarely resulted in the pursued insect leaving the pond. The number of pursuits of *S. striolatum* in tandem by aeshnid males was striking.

Interactions between female aeshnids and males of other species and libellulids

During the whole period of the observations very few occurrences of female aeshnids interacting with other species were recorded. Table 4 includes all the occurrences which were observed. Most records involved female *A. imperator*. Attacks on this species may be more frequent because it oviposits on submerged weed and so is generally more conspicuous than females of other species which oviposit on emergent vegetation or on the bank. The strong attacks by female *A. imperator* show that aggressive behaviour in this species is not confined to males. It appeared to be aimed at preventing interference with oviposition.

Anomalous behaviour

Anomalous behaviour was occasionally observed. A male *A. cyanea* was observed attempting to mate with another male of its own species. A male *A. mixta* flew round the pond attached to a female *A. cyanea*. Another male *A. mixta* attempted to mate with a *S. striolatum* and an *A. cyanea* with a pair of *S. striolatum* in tandem.

An *A. grandis* was seen attacking a copulating *A. mixta* on two occasions and a pair of *A. mixta* in tandem with the female's abdomen hanging down once. An *A. cyanea* was seen to attack a pair of *A. grandis* in the same position.

Table 3. Outcome of interactions between male aeshnids and libellulids.

Pursuing species	Pursued species	Number of encounters (number of occasions pursued species driven from pond)
Aeshnids	Libellulids	
A. imperator	*L. quadrimaculata*	10(0)
A. imperator	*O. cancellatum*	1(0)
A grandis	*L. quadrimaculata*	5(1)
A. grandis	*S. striolatum*	18(2)
A. grandis	*S. striolatum* in tandem	19(2)
A. cyanea	*L. quadrimaculata*	3(1)
A. cyanea	*S. striolatum*	24(0)
A. cyanea	*S. striolatum* female	1(0)
A. cyanea	*S. striolatum* in tandem	9(0)
A. mixta	*S. striolatum*	30(0)
A. mixta	*S. striolatum* female	1(0)
A. mixta	*S. striolatum* in tandem	26(0)
B. pratense	*L. quadrimaculata*	2(0)
Libellulids	Aeshnids	
L. quadrimaculata	*A. imperator*	10(0)
L. quadrimaculata	*A. grandis*	7(0)
L. quadrimaculata	*A. cyanea*	7(1)
L. quadrimaculata	*B. pratense*	1(0)
S. striolatum	*A. grandis*	7(1)
S. striolatum	*A. cyanea*	7(1)
S. striolatum	*A. mixta*	12(1)

These observations refer to sample counts only: many other aeshnid/libellulid interactions were observed but not recorded.

Discussion

Implications of pond size

Before the nature of heterospecific encounters can be discussed we have to ask whether conclusions on the behaviour of male aeshnids on small ponds are applicable to those on larger waterbodies. Small isolated ponds differ significantly from large ones in two ways.

Table 4. Outcome of heterospecific interactions between male aeshnids and female aeshnids and between female aeshnids and male libellulids.

Pursuing species	Pursued species	Number of encounters (number of occasions the pursued species was driven from pond)
A. grandis male	*A. imperator* female	6(0)
A. cyanea male	*A. imperator* female	4(2)
A. imperator female	*A. grandis* male	2(1)
A. imperator female	*A. cyanea* male	2(2)
A. imperator female	*L. quadrimaculata* male	11(3)
L. quadrimaculata male	*A. imperator* female	9(0)
L. quadrimaculata male	*A. cyanea* female	2(1)

First they tend to have relatively smaller numbers of potential territory holders in their vicinity, and therefore the number of encounters is likely to be fewer than at larger waterbodies. Secondly, small ponds do not contain suboptimal habitat out of view of territory holders on the pond. As a consequence all encounters result in either the pursued insect leaving the pond or remaining at it. On the other hand at large waterbodies the pursued insect may neither leave nor remain but can retreat to suboptimal habitat out of sight of territory holders. As a result the outcomes of encounters are often less conclusive than at a small pond.

During the period covered by the observations at Swavesey I paid visits to larger ponds, rivers and ditches which supported the same five aeshnid species. It was abundantly clear that heterospecific pursuits occurred in all types of habitat. On the other hand the consequences of the pursuits were often less clear cut than at the Swavesey pond, as was to be expected: often the pursued insect would neither remain nor leave but would move to a distant part of the waterbody, which to the human observer appeared to provide a suboptimal habitat.

It is concluded that while differences between small and large waterbodies must have some effect on the populations observed, they can have little bearing on the nature of heterospecific encounters.

The nature of heterospecific encounters

This study shows that much of the time and energy of male aeshnid dragonflies is spent on heterospecific pursuit. This suggests that it must have strong survival value. What is it? Does heterospecific pursuit confer some positive advantage as it does among some vertebrates, when a shared resource, such as food or nesting site is in short supply? Among species which perch by their territories there can be competition for especially

favourable perching places (Rehfeldt & Hadrys 1988). This is relevant to libellulids but not to most aeshnids. By reducing the number of heterospecific males in the territory there would be less distraction from reacting decisively when a conspecific rival or mate arrives. Conceivably heterospecific pursuits might reduce competition for food if or when feeding by water is significant. If the number of males and hence the number of successful matings by other species were reduced the number of larval competitors might be reduced. This study shows that the outcome of heterospecific pursuits is variable, and although larger species tend to cause smaller ones to leave the pond, the latter usually return sooner or later. Therefore the effects of heterospecific encounters on reproduction or food supply are unlikely to be very significant. Does this mean, as Singer maintains, that heterospecific pursuits can be explained simply by the fact that male dragonflies cannot afford to hesitate when intruders enter their territories?

If Singer is correct one would expect all male dragonflies initially to pursue conspecific and heterospecific males with equal determination. Then, when the pursuing male was close to the pursued male it would identify it and would either attack it if it were conspecific or would stop chasing it if it belonged to another species because fighting can lead to injury. That heterospecific pursuits generally do not result in determined attacks on other species gives support to Singer's hypothesis. However, other observations made in this study do not support it. They show that males generally pursue their own species much more vehemently than heterospecific species. This and the fact that they often behave differently when they see insects markedly different from themselves strongly suggest that aeshnids can, to some extent at least, differentiate between their own and other species when quite distant from them. Further, the pursuing insect does not always break off its pursuit when it is close to a heterospecific male: sometimes it pursues it fiercely or even attacks it. It is concluded that while Singer's hypothesis is partly supported by these studies, it does not explain completely what is observed in the field.

Two different types of explanation of heterospecific pursuits are suggested. Firstly, dragonflies often react inappropriately to suboptimal stimuli. Notably males quite frequently attempt to mate with males of their own species and sometimes with females of other species (see for example p. 10-11). Vigorous attacks by males on heterospecific males may simply be examples of reactions to suboptimal stimuli when drive is high. This may be the explanation in some cases but vigorous heterospecific pursuits seem to be too numerous to be accounted for in this way. Therefore an alternative explanation which is consonant with all the facts is suggested.

The successful ousting of rival conspecifics involves quite complicated behaviour, which has purely instinctive elements, but success in positioning the insect to its rival and to microtopography could be greatly increased by learning from experience. If this is the case practice in attacking would be valuable and have considerable survival value. It is suggested that practising aggressive skills may be one and perhaps the principal function of heterospecific pursuit.

The different explanations of heterospecific pursuit are not mutually exclusive. It is always unwise to assume that any one activity provides only one type of selective advantage. By pursuing heterospecifics male aeshnids may benefit by improving their aggressive skills as well as by not losing opportunities to oust their rivals.

Acknowledgements

I am grateful to Janet Moore and the referee for helpful criticism of the manuscript.

References

Corbet, P.S., 1999. Dragonflies: Behaviour and Ecology of Odonata. Harley Books, Great Horkesley, Colchester. 829 pp.

Frantsevich, L.I. & P.A. Mokrushov, 1984. Visual stimuli releasing attack of a territorial male in *Sympetrum* (Anisoptera: Libellulidae). Odonatologica 13: 335–350.

Hammond, C.O., 1983. The Dragonflies of Great Britain and Ireland. 2nd ed. rev. by R. Merritt, Harley Books, Great Horkesley, Colchester. 116 pp.

Kaiser, H., 1974. Verhaltensgefüge und Temporialverhalten der Libelle *Aeschna cyanea* (Odonata). Zeitschrift für Tierpsychologie 34: 398–429.

Moore, N.W., 1964. Intra- and interspecific competition among dragonflies (Odonata): an account of observations and field experiments on population density control in Dorset. 1954–60. Journal of Animal Ecology 33: 49–71.

Moore, N.W., 1987. The Bird of Time: the science and politics of nature conservation – a personal account. Cambridge University Press, Cambridge. 290 pp.

Pajunen, V.I., 1962. A description of aggressive behaviour between males of *Leucorrhinia dubia* (Vander Linden) (Odon., Libellulidae). Annales Entomologici Fennici 28: 108–118.

Pajunen, V.I., 1964. Aggressive behaviour in *Leucorrhinia caudalis* (Charpentier) (Odon., Libellulidae). Annales Zoologici Fennici 1: 357–369.

Pajunen, V.I., 1966. The influence of population density on the territorial behaviour of *Leucorrhinia rubicunda* (Linaeus) (Odon., Libellulidae). Annales Zoologici Fennici 3: 40–52.

Peters, G., 1972. Gibt es Konkurrenz zwischen Libellenarten (Odonata)? Entomologische Berichten, Berlin. 1972(2): 104–107.

Rehfeldt, G.E. & H. Hadrys, 1988. Interspecific competition in sympatric *Sympetrum sanguineum* (Müller) and *S. flaveolum* (Linnaeus) (Anisoptera: Libellulidae). Odonatologica 17: 213–225.

Singer, F., 1987. Interspecific aggression in dragonflies – a perceptful constraints hypothesis. American Zoologist 27: 49A.