

**THERMOREGULATION IN THREE SPECIES OF
DAMSELFLIES, WITH NOTES ON TEMPORAL
DISTRIBUTION AND MICROHABITAT USE
(ZYGOPTERA: LESTIDAE)**

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Thermoregulation in *Lestes d. disjunctus* Selys, *L. rectangularis* Say, and *L. dryas* Kirby was investigated at the Old Mill Pond, Pictou Landing, Nova Scotia, Canada between 30 July and 3 Sept. 1994. *L. dryas* was more dependent on ambient temperature than *L. disjunctus* and *L. rectangularis*. *L. disjunctus* and *L. dryas* had different temporal distributions and they varied in their microhabitat use. *L. disjunctus* was the first sp. to begin activity during the day (0900 to 1200 h), while *L. dryas* was only active during the afternoon (1200 to 1600 h). *L. disjunctus* perched in full sun in open areas with low grassy vegetation. *L. dryas* was found in shady regions where shrubs were dominant. It had slightly lower thoracic and abdominal temperatures than the other 2 spp.

INTRODUCTION

Dragonflies have been the focus of many thermoregulation studies (MAY, 1976, 1977, 1978, 1991; DE MARCO & RESENDE, 2002; DE MARCO et al., 2005). However, most studies have focused on the suborder Anisoptera. Thermoregulation in the suborder Zygoptera, including the Lestidae, has been largely overlooked.

Damselflies in the genus *Lestes* can be classified as ‘perchers’ (CORBET, 1980), spending most of their time perching on vegetation near the water’s edge. Instead of thermoregulating endogenously, *Lestes* spp. rely on an external heat source,

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carrying out ectothermic regulation behaviorally (WATANABE & TAGUCHI, 1993). According to CORBET (1980), perchers adjust posturally to varying amounts of incident radiation. During high ambient temperatures, *Lestes* spp. seek shade, allowing their bodies to maintain a more or less constant temperature (MAY, 1978). However, under low ambient temperatures, *Lestes* spp. perch so that their entire bodies are in direct sunlight, exposed to maximal solar radiation (WATANABE & TAGUCHI, 1993).

This study focused on measuring body temperature in three sympatric congeners, *Lestes d. disjunctus* Selys, *L. rectangularis* Say and *L. dryas* Kirby at a pond in Pictou Landing, Nova Scotia, Canada, in summer 1994. Although the three species are sympatric in Nova Scotia, they occupy different geographical ranges in North America. *Lestes d. disjunctus*, the most widespread *Lestes* in temperate North America (WESTFALL & MAY, 1996), commonly flies from mid-July to late September near ponds and marshy areas (WALKER, 1953). It occurs as far north as Anchorage, Alaska, the Mackenzie District in the Northwest Territories, and Newfoundland, south to Massachusetts, Indiana and Washington, and along the mountains to Colorado and Arizona. *L. rectangularis* flies from late June to early September, primarily in shaded areas along the perimeter of bog lakes and streams, and, in the southern part of its range, in marshy waters (GOWER & KORMONDY, 1963). It reaches its northern limits in Nova Scotia, western Ontario and North Dakota, and extends south to Kansas, Oklahoma, Alabama and Florida (WALKER, 1953). It is probably the most abundant *Lestes* of the northeastern United States (WESTFALL & MAY, 1996). *L. dryas* emerges in late May or early June and flies until early September (WALKER, 1953). It breeds in permanent marshy or wooded ponds but may frequent temporary ponds as well (WESTFALL & MAY, 1996). In North America, it ranges from Nova Scotia to Quebec, the Northwest Territories, and south to Tennessee and California. It also occurs in Europe and Asia (WALKER, 1953).

The co-occurrence of these three species at a single study site allowed us to explore thermoregulatory differences that might reflect the species' different overall geographic distributions. In addition, we also examined their temporal distribution and microhabitat use since these factors affect thermoregulation.

METHODS

Observations were made on 13 days between 30 July and 3 September 1994 at the Old Mill Pond, Pictou Landing, Pictou County, Nova Scotia, Canada (45°40'N, 62°40'W). The pond was approximately 500 m² and 50 m above sea level. Except for a few locations where depth reached 2 m, most of the pond was less than 1 m deep. The bottom consisted of hard clay with a layer of decaying vegetation ~10 cm thick. A total of 81 numbered wooden stakes were placed every 2 m around its perimeter to allow the location of each damselfly to be described accurately. Shoreline vegetation varied, with sedges and grasses dominating the northern perimeter. Shrubs including *Spiraea latifolia* (Ait.) and *S. tomentosa* L. were common along the rest of the perimeter. The pond was surrounded by *Picea glauca* (Moench) Voss, *Betula alleghaniensis* Britt., and *Populus tremuloides* Michx. which shaded the

study site. Emergent vegetation (*Carex* sp.) was only present in the northern and eastern reaches of the pond.

BEHAVIORAL OBSERVATIONS – Data were obtained from 0900 to 1600 h on warm sunny days when damselflies appeared at the pond. Days with cooler temperatures and rain were not included in the study since damselflies could not be found during those conditions. Daily onset of activity for each species was recorded throughout the study. A walk around the periphery of the pond was done each hour to avoid bias.

Individual damselflies were visually located around the periphery of the pond. Once spotted, each damselfly was continually observed for 10 min. Time of observation and the exact location of each individual, as determined by stake number, were noted. Time in flight was measured with a stopwatch. If a damselfly was perched during the observation, the species of vegetation was recorded and placed in one of four groups: (1) grass, (2) sedge, (3) *Spirea* spp., and (4) other. Less abundant vegetation such as *B. alleghaniensis*, *Solidago canadensis* L., *Aster* spp., and *P. glauca* were placed in the “other” category. The amount of light exposure of the perch was classified and recorded as: full sun or partial/full shade.

BODY AND AMBIENT TEMPERATURES – After behaviors were recorded, individuals were captured with an aerial insect net and their sex noted. Body temperatures to the nearest 0.1°C were taken with a type-K thermocouple attached to a digital thermometer (Atkins Technical, Inc., Gainesville, Florida). Thoracic temperature was taken on the ventral surface of the third segment of the metasternite, while abdominal temperature was taken on the ventral side of the basal plate. The thorax and abdomen were never penetrated when temperatures were taken. Thoracic temperatures were always recorded before abdominal temperatures. Ambient temperature in the sun and shade were recorded with the same thermocouple immediately after each measurement, and taken ca 10 cm above the ground. If individuals were perched at the time of capture, the surface temperature of vegetation was also recorded by placing the thermocouple on the substrate.

After body temperatures were taken, each damselfly was uniquely numbered on all four wings with a waterproof ink pen (Staedtler Lumocolor 317, Germany) and released, allowing later identification in the field.

A factorial analysis of variance with a complete block design was used to analyze body temperatures (thoracic and abdominal), perching substrate and ambient temperatures among the three species of damselflies. Factorial analysis of variance was also performed to test for differences in temperature between males and females, and between damselflies observed in the morning versus afternoon. Linear regression was used to determine if body temperatures were regulated by behavior and to determine if body temperatures were decoupled from ambient temperatures. A regression slope <1 likely indicates thermoregulation (MAY, 1977).

Chi-square analyses were used to test for differences in sex ratios of each species between morning (0900 to 1200 h) and afternoon (1200 to 1600 h). A *t*-test of equal variance was performed to test for differences between *L. disjunctus* and *L. dryas* in percent time flying during the afternoon. A *t*-test of unequal variance was used to test for differences in percent time flying between morning and afternoon hours for *L. disjunctus*.

For analysis of microhabitat use, a chi-square analysis of frequency counts was used to test for differences in the four perching substrates: grass, sedge, *S. latifolia*, and “other”. Chi-square tests were also used to compare the proportions of *L. disjunctus* and *L. dryas* basking in the sun and shade. All statistical analyses were performed using SAS software (SAS INSTITUTE, 1996).

RESULTS

ABUNDANCE

Lestes disjunctus was the most abundant species, with a highly skewed sex ratio; 186 individuals (154 males, 32 females) were marked during the course of the study (Tab. I). In contrast, *L. dryas* and *L. rectangularis* occurred in smaller numbers (65 and 17 individuals observed, respectively), with more even sex ratios (1.5 ♂:1.0 ♀ and 0.8 ♂:1.0 ♀, respectively).

AMBIENT TEMPERATURES

Mean (\pm s.e.) ambient temperatures throughout the study in the sun and shade were $25.4 \pm 0.5^\circ\text{C}$ and $22.6 \pm 0.4^\circ\text{C}$, respectively. Ambient temperatures were cooler in the morning (mean \pm s.e. = $22.6 \pm 0.4^\circ\text{C}$) than in the afternoon (mean \pm s.e. = $25.8 \pm 0.4^\circ\text{C}$) ($F_{1,208} = 33.44$, $P < 0.0001$) (Fig. 1). Ambient temperatures at the end of July and the first week of August were higher in comparison to ambient temperatures in mid-August (Fig. 2).

BEHAVIORAL THERMOREGULATION

The proportion of individuals basking in the sun and shade varied among species ($\chi^2 = 9.13$, $P < 0.0025$). For *L. disjunctus*, of 116 observations, 95 were made in areas with full sun exposure, while 21 were observed in shade (or partial shade). In contrast, *L. dryas* were more evenly distributed between sun (18) and shade (14). Too few observations of *L. rectangularis* were available for analysis.

Thoracic temperatures for all three species were significantly lower than abdominal temperatures ($F_{3,748} = 70.33$, $P < 0.0001$) (Tab. II). Although thoracic

and abdominal temperatures overall did not vary among the three species ($F_{6,748} = 1.74$, $P = 0.1093$), *L. dryas* had lower thoracic and abdominal temperatures in comparison to *L. disjunctus* (Tab. II). *L. dryas* also had lower thoracic temperatures in comparison to *L. rectangularis*, however, abdominal temperatures

Table I

The distribution of male and female *Lestes disjunctus*, *L. dryas* and *L. rectangularis* in the morning and afternoon at the Old Mill Pond, Pictou Landing, Nova Scotia, from 30 July to 3 September, 1994

Species	Sex	N	Morning	Afternoon
			0900-1200 h	1200-1600 h
<i>L. d. disjunctus</i>	♂	154	54	100
	♀	32	4	28
<i>L. dryas</i>	♂	39	0	39
	♀	26	0	26
<i>L. rectangularis</i>	♂	8	2	6
	♀	9	5	4
Total		268	65	203

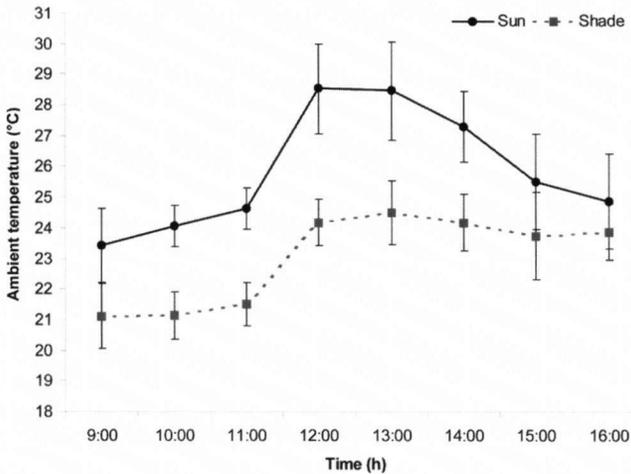


Fig. 1. Mean (\pm s.e.) ambient temperatures in the sun and shade throughout the day (0900 to 1600 h) at the Old Mill Pond, Pictou Landing, Nova Scotia, from 30 July to 3 September, 1994.

were the same (Tab. II). The temperature of the perching substrates was higher for *L. dryas*, and unlike the other two species, exceeded the ambient temperatures. Thoracic and abdominal temperatures were significantly higher than ambient temperatures for all three species. The relationship of body temperature to air temperature is shown in Figure 3. The slopes of the regression lines for abdominal and thoracic temperatures for *L. dryas* were not significantly different from 1 (see legend of Fig. 3 for regression equations). *L. disjunctus* and *L. rectangularis* had slopes significantly different from 1, indicating that body temperatures are less dependent on ambient temperature.

Males of *L. disjunctus* and *L. rectangularis* tended to have slightly higher thorax and abdominal temperatures than females (Tab. III), but these temperatures, including perching and ambient temperatures, for all three species were not signifi-

Table II

Mean thoracic and abdominal temperatures of *Lestes disjunctus*, *L. dryas* and *L. rectangularis* and their corresponding perching substrate and ambient temperatures taken between 0900 to 1600 h

Species	n	Mean \pm s.e. temperature ($^{\circ}$ C)			
		Thoracic	Abdominal	Perching substrate	Ambient
<i>L. disjunctus</i>	148	27.5 \pm 0.3a	29.2 \pm 0.3a	22.9 \pm 0.3b	23.5 \pm 0.2a
<i>L. dryas</i>	38	26.1 \pm 0.6b	27.8 \pm 0.6b	24.1 \pm 0.8a	22.4 \pm 0.3b
<i>L. rectangularis</i>	15	28.0 \pm 0.8a	29.1 \pm 0.8ab	22.4 \pm 0.8b	23.8 \pm 0.5a
Mean		27.2 \pm 0.2	28.7 \pm 0.3	23.1 \pm 0.4	23.2 \pm 0.3

Means in the same column followed by a different letter are significantly different (LSMEANS, SAS Institute 1996) at $\alpha = 0.05$.

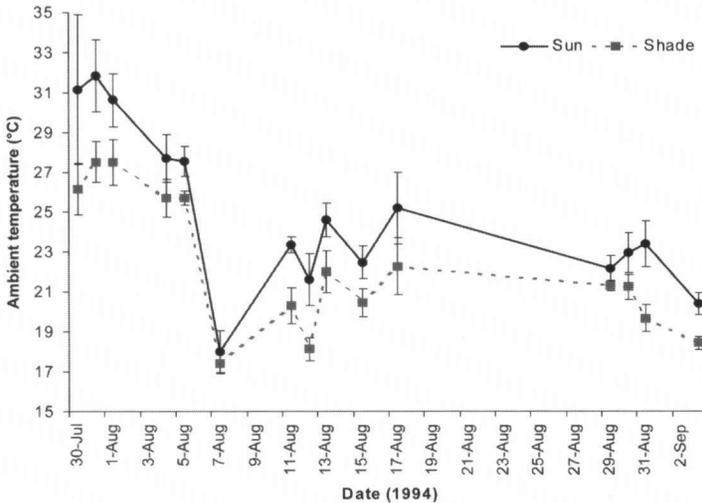


Fig. 2. Mean (\pm s.e.) ambient temperatures in the sun and shade throughout the study period (30 July to 3 September, 1994) at the Old Mill Pond, Pictou Landing, Nova Scotia.

cantly different between males and females ($F_{6, 720} = 0.50$, $P < 0.8094$). Thoracic and abdominal temperatures also did not vary between morning and afternoon hours ($F_{3, 720} = 0.73$, $P < 0.5339$) (Tab. III).

TEMPORAL DISTRIBUTION

L. disjunctus occurred throughout the study period. In contrast, *L. dryas* and *L. rectangularis* were not present until August 11th and 12th, respectively. Daily onset of activity differed distinctly between the species. *L. disjunctus* became active during morning (0900 to 1200 h) (Fig. 4). *L. dryas* was never observed during morning. Onset of activity for *L. rectangularis* appeared to vary throughout the study, although numbers were small.

In general, more damselflies were observed during afternoon (1200 to 1600 h) than morning (0900 to 1200 h) (Tab. I). This was true for both sexes (females: $\chi^2 = 69.4$, $P < 0.001$; males: $\chi^2 = 19.10$, $P < 0.001$), except in *L. rectangularis*, in which female numbers were similar in morning and afternoon. There was a temporal shift in sex ratio for *L. disjunctus*, with sex ratios of 13.5 ♂:1.0 ♀ and 3.8 ♂:1.0 ♀ during morning and afternoon, respectively.

L. disjunctus and *L. dryas* spent an average (\pm s.e.) of $4.2 \pm 0.6\%$ ($n = 65$) and $3.4 \pm 1.3\%$ ($n = 7$) of their time flying, respectively. Both species flew equally during the afternoon ($t = -1.20$, $df = 34$, $P = 0.2384$). However, *L. disjunctus* spent more time flying in the afternoon (mean \pm s.e. = $6.4 \pm 1.1\%$) than in the morning (mean \pm s.e. = $2.8 \pm 0.5\%$) ($t = 2.89$, $df = 37$, $P < 0.0064$).

MICROHABITAT USE

L. disjunctus and *L. dryas* showed differential habitat use around the pond. *L. dryas* was found in areas where shrubs were dominant and near shaded stakes 1-6 during the afternoon (1200 to 1600h), while *L. disjunctus* was more commonly found in open areas where low grassy vegetation was present (Fig. 5). *L. rectangularis* was not included in this analysis due to low numbers.

L. disjunctus and *L. dryas* differed significantly in their choice of perching substrate ($\chi^2 = 46.7$, $P < 0.0001$). In 160 observations, *L. disjunctus* perched primarily on grass (0.72) and secondarily on *S. latifolia* (0.19), sedge (0.07) and "other" vegetation (0.02). In 43 observations, *L. dryas* perched primarily on grass (0.35) and sedge (0.35) and secondarily on "other" vegetation (0.19) and *S. latifolia* (0.11).

DISCUSSION

Lestes dryas was more dependent on ambient temperature than *L. disjunctus* and *L. rectangularis* (Fig. 3). These differences in dependencies on ambient temperature correlate with each species' behavior. *L. disjunctus* and *L. dryas* had different temporal distributions and they also varied in their microhabitat use. By perching in full sun, *L. disjunctus* was able to elevate temperatures above ambient temperature, allowing it to be the first species to begin activity during the day. *L. disjunctus*

Table III

Mean thoracic and abdominal temperatures of male and female *Lestes disjunctus*, *L. rectangularis* and *L. dryas* and their corresponding perching substrate and ambient temperatures taken in the morning (0900 to 1200 h) and afternoon (1200 to 1600 h)

Time of day	Sex	N	Mean \pm s.e. temperature ($^{\circ}$ C)			Ambient
			Thoracic	Abdominal	Perching substrate	
<i>Lestes d. disjunctus</i>						
Morning	♂	28	28.1 \pm 0.5a	31.1 \pm 0.5a	22.5 \pm 0.6b	23.9 \pm 0.5a
	♀	4	26.8 \pm 1.3ab	28.6 \pm 1.4b	21.6 \pm 1.3b	22.7 \pm 1.2ab
Afternoon	♂	83	27.7 \pm 0.4a	29.1 \pm 0.4b	23.1 \pm 0.3b	23.5 \pm 0.2a
	♀	28	26.4 \pm 0.7b	28.1 \pm 0.7bc	22.8 \pm 0.4b	23.5 \pm 0.4a
<i>Lestes dryas</i>						
Afternoon	♂	24	26.0 \pm 0.7b	27.8 \pm 0.8b	23.6 \pm 0.8b	22.3 \pm 0.6b
	♀	13	26.4 \pm 1.8b	27.6 \pm 1.0bc	25.3 \pm 1.3a	22.6 \pm 0.8ab
<i>Lestes rectangularis</i>						
Morning	♂	1	24.8	27.1	23.3	20.3
	♀	5	30.0 \pm 1.8a	31.6 \pm 1.1a	22.2 \pm 0.6bc	24.6 \pm 1.1a
Afternoon	♂	5	28.8 \pm 0.5a	28.9 \pm 0.4b	22.9 \pm 0.7b	23.9 \pm 0.7a
	♀	4	25.2 \pm 0.9b	26.6 \pm 1.7c	21.6 \pm 0.1c	23.5 \pm 0.7ab

Means in the same column followed by a different letter are significantly different (LSMEANS, SAS Institute 1996) at $\alpha = 0.05$.

tus and *L. rectangularis* were active throughout the day. In contrast, the poorly thermoregulating species, *L. dryas*, was found only during the warmer afternoon. MAY (1977) found similar patterns in *Micrathyrja* spp.; those that thermoregulated well were active for extended periods, while those with poor thermoregulation were active only during midday. DE MARCO (1998) suggests sun basking may not be necessary for those species found in shade when temperatures in the area are near optimum. Differences in behavior resulted in slight differences in body

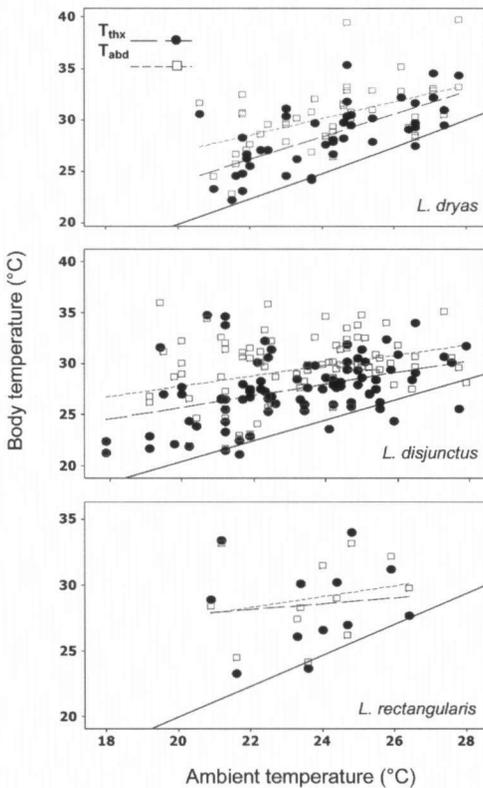


Fig. 3. Relationship of body temperature (T_b) to air temperature (T_a) in three species of *Lestes*. The solid, oblique line shows where $T_b = T_a$. Regression equations (dotted line = abdominal temperatures; dashed line = thoracic temperatures) are as follows: *L. dryas*, abdomen- $T_b = 10.6 + 0.812 (T_a)$, $r = 0.516$, $n = 47$; thorax- $T_b = 1.88 + 1.10 (T_a)$, $r = 0.698$, $n = 47$; *L. disjunctus*, abdomen- $T_b = 17.6 + 0.508 (T_a)$, $r = 0.351$, $n = 88$; thorax- $T_b = 14.3 + 0.571 (T_a)$, $r = 0.423$, $n = 88$; *L. rectangularis* abdomen- $T_b = 19.3 + 0.408 (T_a)$, $r = 0.721$, $n = 12$; thorax- $T_b = 23.3 + 0.222 (T_a)$, $r = 0.361$, $n = 12$.

temperatures, with *L. dryas* having slightly lower thoracic and abdominal temperatures than *L. disjunctus* and *L. rectangularis*.

L. disjunctus aggregated near stakes 1 to 37; *L. dryas* was more evenly dispersed, although 71% of sightings occurred between stakes 62 and 6 (Fig. 5). Although both species aggregated near stakes 1 to 6, due to their distinct diel patterns they were temporally segregated. *L. dryas* was common in this grassy area only in the afternoon when stakes 1 to 6 were shaded from the afternoon sun. *L. disjunctus* was found at these sites only in the morning when stakes 1 to 6 were entirely exposed to the sun. Communal oviposition occurred for both species at stakes 1 to 6 where grass and reeds were dominant. This is similar to BICK & BICK (1965) who studied the oviposition sites for *Argia apicalis* (Say) (Zygoptera: Coenagrionidae) and noticed that most oviposition took place in communal sites, limited to a few suitable locations.

Sex ratios for *L. disjunctus* were male biased. These results are similar to ROBB et al. (2006) who also showed male-biased sex

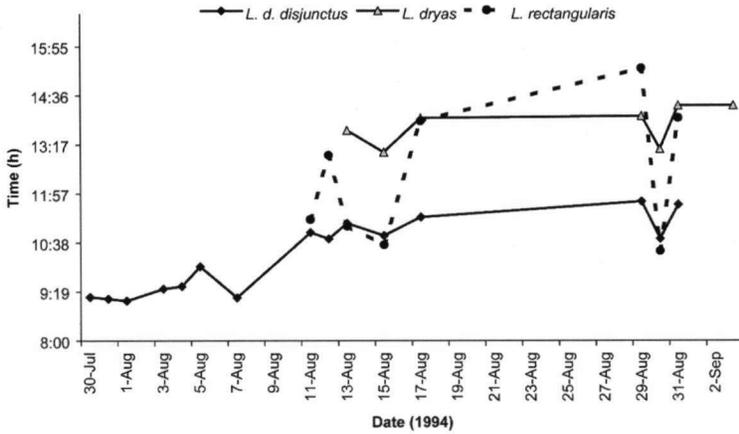


Fig. 4. Daily onset of activity for *Lestes disjunctus*, *L. dryas*, and *L. rectangularis* at the Old Mill Pond, Pictou Landing, Nova Scotia, from 30 July to 3 September, 1994.

ratios for *L. disjunctus*. This biased sex ratio was most likely due to females avoiding breeding habitats (FOSTER & SOLUK, 2006) at particular times of day. Daily onset of activity differed between males and females, as reflected by the temporal shift in sex ratio from morning to afternoon; males became active during morning but females were not seen in large numbers until afternoon. UTZERI & ERCOLI (2004) noted similar behavior for *Lestes virens* (Charpentier). CORBET (1980) describes this as a general odonate behavior, with mature males arriving at the pond earlier in the day. In this study, the differences in onset of activity throughout the day between the sexes were not related to temperature. Although thoracic and abdominal temperatures of *L. disjunctus* and *L. rectangularis* differed slightly between males and females, ambient temperatures to which males were exposed in the morning did not differ significantly from those encountered by females in the afternoon. Since copulation only occurs at the pond (CORBET, 1980), males may increase their reproductive success by arriving early near copulation sites.

If *Lestes* spp. are similar to *Argia apicalis* where females avoid a second copulation (BICK & BICK, 1965), to ensure maximum reproductive success, it would be an advantage for the female to defer mating activity to the afternoon. Females would reduce the amount of time harassed by males, which they would encounter in greater frequency earlier in the day. Since more *L. disjunctus* females were present in the afternoon, mating activity was likely more frequent, which would account for the increased flying activity observed in afternoon.

L. disjunctus and *L. rectangularis* males tended to have slightly higher thoracic and abdominal temperatures than females. These results are similar to ISHIZAWA (1998) where males of *Sympetrum frequens* (Selys) (Anisoptera: Libellulidae) had

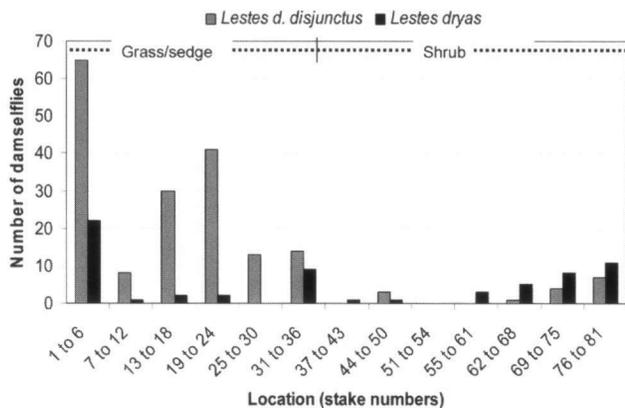


Fig. 5. Frequency distribution of *Lestes disjunctus* ($n = 186$) and *L. dryas* ($n = 65$) in relation to microhabitats of grass/sedge and shrub (stakes numbered 1 to 81) around the Old Mill Pond, Pictou Landing, Nova Scotia, observed 30 July to 3 September, 1994.

higher thoracic temperatures than females. MAY (1978) reported that body size in dragonflies has a major influence on thermoregulation. These sexual differences in body temperatures might be due to differences in body size between the sexes (ISHIZAWA, 1998), although in this study we did not measure body size.

MAY (1986) found that the thoracic body temperatures of *Anax junius* (Drury) (Anisoptera: Aeshnidae) were higher than abdominal temperatures due to the generation of heat by the flight muscles. Our results differ from MAY (1986) with thoracic temperatures in all three species significantly lower than abdominal temperatures. Unlike *A. junius* which is considered to be a flyer (HEINRICH, 1993), lestids spend most of their time perching. With this subdued lifestyle, the abdomen has time to absorb solar radiation, and thoracic muscles are rarely exercised. This in combination with the relatively smaller surface to volume ratio of the thorax would make it more susceptible to heat loss, which could have accounted for the difference in abdominal and thoracic temperatures.

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