

Trogus parasitoids of *Papilio* butterflies undergo extended diapause in western Canada (Hymenoptera, Ichneumonidae)

Julian R. Dupuis¹, Boyd A. Mori², Felix A.H. Sperling¹

1 Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada **2** Agriculture and Agri-Food Canada, Saskatoon Research and Development Centre, Saskatoon, Saskatchewan, Canada

Corresponding author: Julian R. Dupuis (jrdupuis@ualberta.ca)

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Abstract

Diapause that extends across multiple years is considered a bet-hedging strategy in insect species that are exposed to unfavorable environmental conditions. The dynamics of extended diapause in herbivores can be complicated when their parasitoids can also extend diapause, although our knowledge of these dynamics is based primarily on pest species. Here, we report on regional variation in the phenology and life history of *Trogus* parasitoids of *Papilio machaon* group swallowtail butterflies in western Canada. We observed flexible phenological patterns in this interaction, with both hosts and parasitoids undergoing extended diapause. Additionally, we documented parasitism of earlier instar larvae in these *Trogus* species, which to our knowledge has not been observed in North America. Our observations provide a foundation for studying the potential evolutionary consequences of extended diapause in these multispecies interactions.

Keywords

Trogus lapidator, *Trogus fulvipes*, *Papilio machaon*, *Papilio zelicaon*, extended diapause, phenology

Introduction

Diapause is a vital life history characteristic for many insects that cope with harsh environmental conditions (Chapman 1998). At northern latitudes this period of developmental delay facilitates winter survival and is usually initiated or terminated by photoperiod and/or temperature cues (Denlinger 2002). Although the temporal dynamics of diapause are predictable and regular in some species, others exhibit plasticity where some individuals go through prolonged diapause periods that last multiple years (Tauber et al. 1986, Danks 1987, Hanski 1988). Such extended diapause is considered an adaptive “bet-hedging” strategy, providing long-term evolutionary gains at the expense of short-term costs (e.g. Menu and Debouzie 1993, Danforth 1999, Hopper 1999, Soula and Menu 2005).

The dynamics of facultative extended diapause are complicated by multispecies interactions, such as those between parasitoids and their hosts, each of which may exhibit extended diapause (Hanski 1988). In some cases these diapause periods are tied to similar external cues (Annala 1981), while in others the parasitoids simply follow the phenology of their host, whether it is simple or prolonged (Martinek 1985). Population modeling of these systems shows that length of diapause and proportion of parasite and host individuals extending their diapause can positively or negatively influence the stability of host-parasitoid interactions (Ringel et al. 1998, Corley et al. 2004). These predictions and most knowledge of extended diapause dynamics in host-parasitoid systems come primarily from insect pest systems, where population dynamics can be eruptive (Wallner 1987). The diverse ecology of parasitoids, particularly in Hymenoptera (LaSalle and Gauld 1993), underlines the importance of incorporating the dynamics of non-pest species into our understanding of extended diapause.

Trogus is a genus of large koinobiont parasitoid wasps that specialize on swallowtail butterflies (Lepidoptera: Papilionidae) (Sime and Wahl 2002). Single eggs are laid in caterpillars that develop normally through pupation; at this point the wasp larva begins feeding, develops, and pupates within the host pupa. Adults then emerge from the host pupa through the wing pad using primarily liquid secretions to dissolve the host tissue, creating a distinctive exit hole (Shaw et al. 2015). *Trogus* are frequently encountered due to widespread collecting and rearing of swallowtail larvae by lepidopterists, and so their host records are reliable (Wahl and Sime 2006). Despite this, the taxonomy of Nearctic *Trogus* has been contentious, with estimates of the number of species in the Nearctic ranging from one to a dozen (Heinrich 1962, Carlson 1979, Wahl and Sime 2006). Apart from their oviposition and direct interaction with swallowtail butterfly caterpillars (e.g. Sime 2005), the biology of these wasps is relatively unknown.

Here we report phenology and life history observations of *Trogus* spp. in Alberta and British Columbia. Extensive sampling of larvae of the *Papilio machaon* Linnaeus species group in population genetic and phylogeographic surveys (Dupuis and Sperling 2015, Dupuis and Sperling in review) resulted in a substantial number of *Trogus* specimens. We observed several novel life history features for *Trogus*, including extended diapause, absence of diapause, and parasitism of caterpillar hosts at earlier

instars than previously documented in this region. This life history information led us to consider the evolutionary consequences of parasitism and phenology in this host-parasitoid interaction.

Methods

During the summers of 2010–2012, *Papilio* larvae and eggs were hand-collected from larval hostplants in three geographic regions of Alberta and northeastern British Columbia, each of which contained a different member of the *P. machaon* species group (Figure 1). Two regions had subspecies of *P. machaon* whose larvae fed on *Artemisia dracuncululus* L.: *Papilio machaon dodi* McDunnough, 1939 in the Red Deer River valley in southern Alberta, and *P. m. pikei* Sperling, 1987 in the Peace River valley in northwestern Alberta and northeastern British Columbia. The third region was the foothills of the Rocky Mountains, where *P. zelicaon* Lucas, 1852 and putative hybrids between *P. machaon* and *P. zelicaon* (see Dupuis and Sperling 2015; here referred to as *P. zelicaon*) were collected on *Heracleum lanatum* Bartr. from southwestern Alberta to northeastern British Columbia. Larval instar of caterpillars at the time of collection was estimated visually by JRD.

Caterpillars were reared on host plant clippings with a lighting regime of 16 hours light: 8 hours dark, and temperature maintained at 22°C (\pm 2°C). After pupation, an overwintering diapause period was simulated by storing pupae in a refrigerator held at 4°C (\pm 2°C) in total darkness for 16–20 weeks; pupae were misted with water every 1–2 weeks to maintain humidity. Following diapause, eclosion was induced by a return to their former light and temperature regimes, with daily water misting. Particularly at northern latitudes, members of the *P. machaon* group are known to undergo extended natural diapause spanning several winter seasons (Sperling 1987). Therefore if pupae did not eclose after 12–16 weeks but appeared viable (normal color, weight, etc.), the cycle of diapause/eclosion conditions was repeated. Dates of collection, pupation, eclosion, and number of diapause periods were recorded for butterflies and emerged parasites. All *Trogus* specimens were deposited in the E.H. Strickland Entomological Museum at the University of Alberta (UASM#270880–270946).

All data was examined for normality with visualization plots and Shapiro-Wilks tests. The number of days to emergence was measured from the date pupae were removed from the refrigerator, regardless of whether the pupae had previously undergone a simulated diapause regime. The number of days to emergence was transformed ($\ln(x)$) to approach the assumptions of normality. To determine if number of days to emergence differed between sex for either *Papilio* or *Trogus*, the data was pooled across geographic regions. Separate ANOVAs were conducted on both *Papilio* and *Trogus*, with number of days to emergence specified as the response variable and sex specified as the explanatory variable. Another ANOVA was conducted to determine if number of days to emergence differed between *Papilio* and *Trogus*, successive diapause events, or geographic regions. Days to emergence was specified as the response variable and species (*Papilio*/*Trogus*), number of diapause events, geographic region, and their interaction

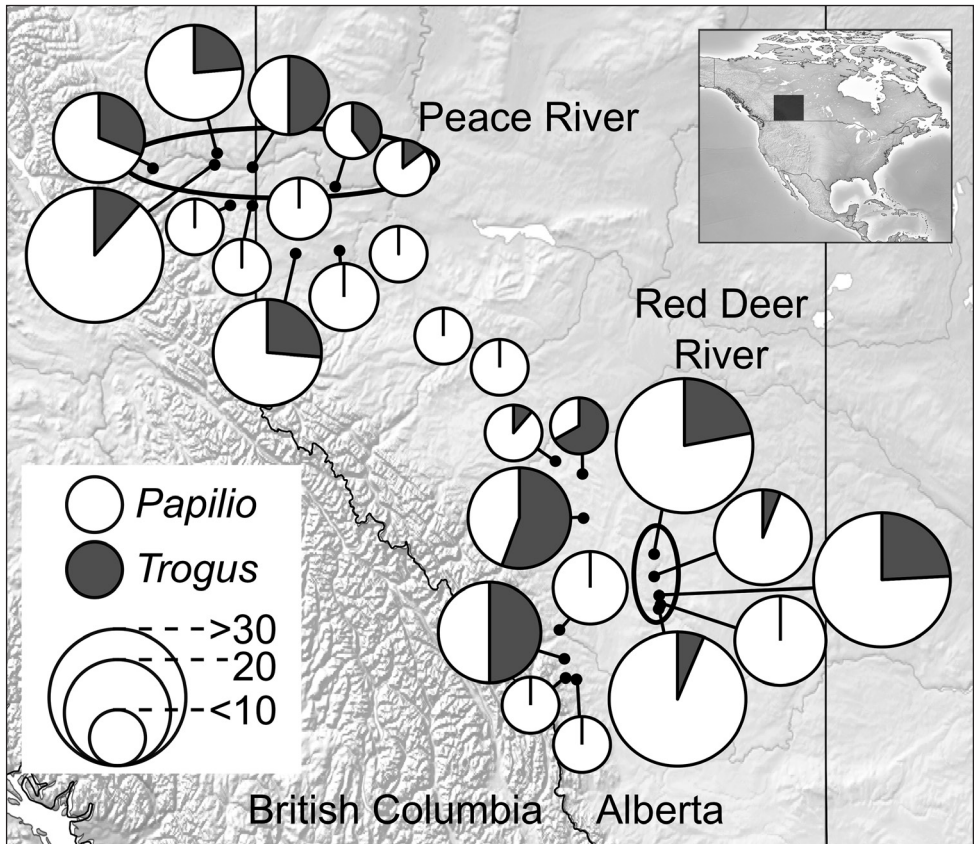


Figure 1. Map of *P. machaon* group larval sampling localities in Alberta and British Columbia. Pie charts represent relative numbers of reared *Papilio* butterflies (white) and *Trogus* parasitoids (grey) per locality (ignoring pupae that did not produce either), and pie chart size reflects sample size of *Papilio* and *Trogus* combined (see inset). Collection regions for *P. machaon* are indicated by ovals: Red Deer River, for *P. m. dodi*, and Peace River, for *P. m. pikei*. All other localities represented *P. zelicaon* collections. Map image is public domain from: www.simplemappr.net.

terms were specified as the explanatory variables. The model was simplified by removal of non-significant variables in a step-wise manner based on the Akaike information criterion (AIC). All statistical analyses were conducted in R 3.2.4 (R Core Team 2016).

Results

In total, 102 eggs and 826 caterpillars were collected during three field seasons. Of these 928 individuals, 685 successfully pupated and produced 290 butterflies and 75 parasites, 66 of which were *Trogus*. Following Wahl and Sime (2006), and after examination of 68 specimens from the Canadian National Collection included in Wahl and

Sime's (2006) revision, 60 individuals that we collected were identified as *T. lapidator* (Fabricius 1787) and the remaining six as *T. fulvipes* Cresson 1868. These species are known to display high variability in western Canada, and putative hybrids between *T. lapidator* and *T. fulvipes* have been collected from some of the same locations as the individuals in this study (Wahl and Sime 2006). This variability and intermediacy between the two species precluded confident species delimitation, and so we conducted statistical analyses on all specimens combined. More detailed taxonomic research is needed to determine the extent of hybridization between these *Trogus* species.

The majority of butterflies went through a single diapause period before eclosion, irrespective of species or collecting region (Table 1). Confirming previous rearing efforts (Sperling 1986), individuals of *P. m. pikei* in the Peace River were more likely than other populations to go through extended diapause before eclosion. One *P. zelicaon* individual did not undergo any diapause and eclosed 43 days after pupation. Although rare at northern latitudes, this is a common phenology in the southern part of the range of *P. zelicaon* where it has multiple flights per year (Scott 1986). Most *Trogus* eclosed after a single diapause period (Table 1), and all identified *T. fulvipes* followed this pattern. However, two individuals of *T. lapidator* reared from *P. zelicaon* did not go through a diapause period, and 11 individuals of *T. lapidator*, mostly reared from subspecies of *P. machaon*, went through two diapause periods before eclosing. To our knowledge, there is only a single previous record of *Trogus* going through multiple diapause periods in this region (Sperling 1986), and we have the first record of *Trogus* species not undergoing overwintering diapause in western Canada. Most *Trogus* were reared from host larvae collected at later larval instars (fourth-fifth); however, several *T. lapidator* were reared from *P. zelicaon* caterpillars collected during their first and second larval instars at Saskatoon Hill, Alberta. *Trogus pennator* (Fabricius 1793), a conspicuous species in eastern North America, is known to oviposit in caterpillars of any age (Sime and Wahl 2002), and *T. violaceus* Mocsáry 1883 (a synonym of *T. lapidator* found in Europe: Wahl and Sime 2006), has been shown to parasitize *P. hospiton* Géné 1839 as early as its second instar (Prota 1962). However, *T. lapidator* and *T. fulvipes* have only been documented from caterpillars collected during later (fourth and fifth) larval instars in western Canada (Sperling 1986, Wahl and Sime 2006). To our knowledge, this is the first record of such early parasitism in these species in North America.

For all *Papilio*, males emerged significantly earlier than females ($F_{1,284} = 9.62$, $P < 0.01$). However, there was no significant difference in emergence time of *Trogus* based on sex ($F_{1,62} = 1.53$, $P > 0.05$). When both *Papilio* and *Trogus* were examined together there was a significant host/parasite (*Papilio*/*Trogus*) by region interaction (Table 2). In the Red Deer River region *Trogus* adults emerged slightly later than *P. m. dodi* adults, whereas in the Peace River region there was no difference in emergence time between *Trogus* and *P. m. pikei* (Figure 2a). In the foothills region, *Trogus* emerged much later than *P. zelicaon* adults. Interestingly, there was no difference in days to emergence in *Papilio* or *Trogus* when number of diapause events was taken into account (Figure 2b). However, the number of days to emergence declined when both *Papilio* and *Trogus* underwent subsequent diapauses (Table 2, Figure 2b).

Table 1. Number of diapause periods for *Papilio* butterflies and *Trogus* parasitoids, summarized by region. RDR: Red Deer River, PR: Peace River.

Host or parasitoid	Region, species/host species	No. diapause periods				Total
		0	1	2	3	
<i>Papilio</i> (host)	RDR, <i>P. m. dodi</i>	0	82	29	6	117
	PR, <i>P. m. pikei</i>	0	48	22	1	71
	Foothills, <i>P. zelicaon</i>	1	75	24	2	102
	Total	1	205	75	9	290
<i>Trogus</i> (parasitoid)	RDR, <i>P. m. dodi</i>	0	11	5	0	16
	PR, <i>P. m. pikei</i>	0	18	4	0	22
	Foothills, <i>P. zelicaon</i>	2	26	1	0	29
	Total	2	55	10	0	67

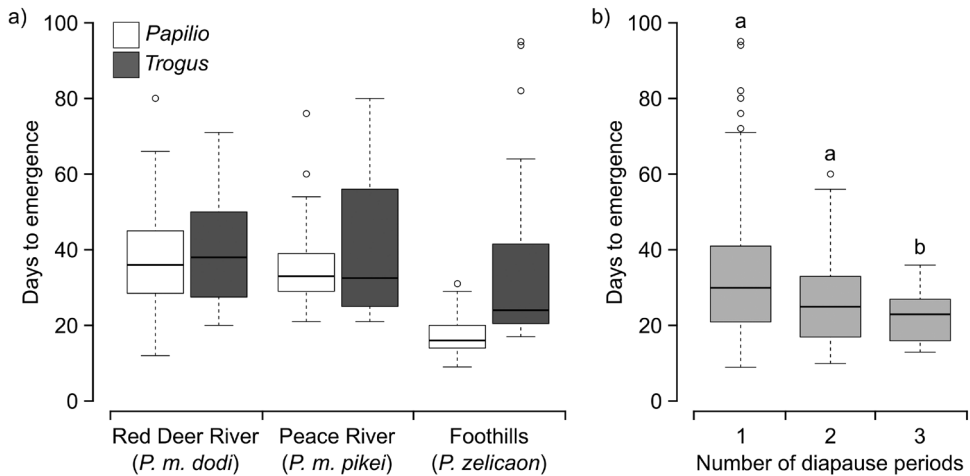


Figure 2. ANOVA results. **a** Number of days to emergence after simulated diapause for *Papilio* and *Trogus* in three geographic regions. There was a significant interaction between number of days to emergence and host/parasite ($P < 0.05$) **b** Number of days to emergence after simulated diapause by number of diapause periods for both *Papilio* and *Trogus* combined. Different letters above boxplots indicate significant differences (Tukey HSD test, $P < 0.05$). For both a and b sections of the figure, the median is indicated by the midline and the bottom and top of the box represent the first and third quartiles, respectively. Whiskers indicate the minimum/maximum values or 1.5 times the interquartile range, whichever is smaller, and circles represent outliers. Untransformed data is presented.

Discussion

Our work on *Papilio machaon* group swallowtail butterflies has fortuitously provided an opportunity to observe the phenology of their *Trogus* spp. parasitoids in western Canada. In addition to observing parasitism in earlier instar hosts than previously

Table 2. ANOVA test results. ANOVA test results for differences in the number of days to emergence between host versus parasite, geographic region, and number of diapause events.

Explanatory variable	DF	F-value	P-value
host/parasite (<i>Papilio/Trogus</i>)	1	25.08	< 0.0001
geographic region	2	154.19	< 0.0001
number of diapause events	2	17.52	< 0.0001
host/parasite*geographic region	2	13.95	< 0.0001
residual	343		

reported for these *Trogus* spp. in this region (Sperling 1987), we have documented a flexible emergence pattern for *T. lapidator*. We collected individuals that did not undergo any overwintering diapause period, as well as several that went through extended diapause before eclosion. *Trogus* emerged later than their hosts, as would be expected given that adult *Trogus* need to oviposit in larval *Papilio*, but this delay varied geographically. This variable phenological pattern of *Trogus* can be interpreted in terms of a potential evolutionary strategy.

Facultative extended diapause is commonly observed in the *P. machaon* group (present study, Sperling 1986), and can be interpreted as an evolutionary strategy for species living in unpredictable environments to withstand unfavorable environmental conditions (drought, irregular precipitation, etc.: Tauber et al. 1986, Danks 1987, Hanski 1988). Although we observed this phenology in all geographic regions in this study, the highest proportion of individuals undergoing extended diapause was observed in *P. m. pikei* in the Peace River region (Table 1). Interestingly, some of the localities in this region also experience very high rates of parasitism by *Trogus* wasps, where similar numbers of *Trogus* and butterflies eclose from reared pupae (Figure 1). Sperling (1986) observed similar patterns at the same localities, and hypothesized that the extended diapause observed in *P. m. pikei* may be an evolutionary strategy to counteract high parasitism rates by decoupling host and parasite phenology. If this is the case, then our observation of extended diapause in *Trogus* parasitoids may indicate that an evolutionary arms race is underway in this system. Under this scenario, *P. m. pikei* are undergoing multiple-year diapauses to avoid parasitism, and *Trogus* are mimicking the same strategy to increase successful parasitism.

In addition to highly parasitized localities in the Peace River region, we observed high parasitism (>50% of reared specimens being *Trogus*) in several populations in the foothills region (Figure 1), a pattern that was not found by Sperling (1986). Despite their comparable rates of parasitism, as well as comparable occurrences of extended diapause in the host, *P. zelicaon*, fewer *Trogus* went through extended diapause in these populations (Table 1). Thus *Trogus* are present in these populations, the hosts may be exhibiting parasite avoidance (following the hypothesis of an arms race), but the parasitoids have not responded with the same phenological flexibility as with *P. m. pikei*. However, we also observed the largest delay between host and parasitoid emergence in

the foothills region (Figure 2a), which may indicate that the overall phenology of these regions differs enough to preclude direct comparison.

Several lines of evidence may explain the overall phenological discrepancies between hosts and parasitoids in these regions. The most obvious is that environmental cues for initiation and termination of diapause may differ between host species/subspecies, as well as between hosts and parasitoids. In the *P. machaon* species group, photoperiod has been identified as the main factor affecting diapause induction (*P. machaon*: Shimada 1983; *P. zelicaon*: Sims 1980; *P. polyxenes* Fabricius 1775: Oliver 1969, Sims 2007), but termination of diapause may also be affected by photoperiod and temperature (*P. polyxenes*: Oliver 1969). Regional differences in diapause dynamics (including degree days required for development) and voltinism are evident across the ranges of the species in this group, but populations in western Canada generally exhibit highly variable and overlapping phenological characteristics (Sperling 1987). Less is known about hymenopteran parasitoids, particularly species without obvious economic impacts. Temperature, combined with variables such as photoperiod and host instar, predominately affects diapause induction and termination in some parasitoids (Ichneumonidae: Griffiths 1969, Eliopolous and Stathas 2003; Trichogrammatidae: Laing and Corrigan 1995), however these effects can vary with the life stage of the insect (Trichogrammatidae: Ivanov and Reznik 2008). It is likely that differences in diapause cues can explain, at least in part, the variable phenologies we observed here. However, if diapause in *Papilio* and *Trogus* depends on regionally variable and species specific combinations of photoperiod and temperature, then extensive research efforts will be required to disentangle those effects.

Several additional factors affect the interpretation of these results. First, documenting *Trogus* phenology was not the main purpose of our collecting efforts. Although we aimed for standardized rearing conditions, we did not tailor rearing conditions of individuals to that of their respective regional environments. Dedicated experimentation mimicking more natural conditions, along with larger sample sizes and collections at particular larval instars, will be valuable for advancing understanding of this interaction. Second, although *Trogus* are specialist parasitoids on swallowtail butterflies, another swallowtail butterfly, *Papilio canadensis* Rothschild and Jordan 1906, also inhabits these areas (Scott 1986). While *Trogus lapidator* has not been reared from *P. canadensis*, there are records of *T. fulvipes* from this host (Sime and Wahl 2002), which adds another layer of complexity to the population dynamics of these parasitoids. Finally, as noted earlier, the taxonomy of these *Trogus* spp. is not well resolved in western Canada, and hybridization between *T. lapidator* and *T. fulvipes* may be widespread; this process may also parallel hybridization between *P. machaon* and *P. zelicaon* (Sperling 1987, Sperling 1990, Dupuis and Sperling 2015, Dupuis and Sperling in review). Detailed taxonomic research will be essential to expanding the hypothesis of an evolutionary arms race, as well as general life history knowledge of these charismatic parasitoids. Our natural history observations should provide a foundation for future work on the *Papilio-Trogus* interaction in western Canada.

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References

- Annala E (1981) Fluctuations in cone and seed insect populations in Norway spruce. *Communications Instituti Forestalis Fenniae* 101: 1–32.
- Carlson RW (1979) Family Ichneumonidae. In: Krombein KV, Hurd PD, Smith DR, Burks BD (Eds) *Catalog of Hymenoptera of America North of Mexico 1*. Smithsonian Institution Press, Washington DC, 315–741.
- Chapman RF (1998) *The Insects: Structure and Function* (4th ed.). University Press, Cambridge, 770 pp. doi: 10.1017/cbo9780511818202
- Corley JC, Capurro AF, Bernstein C (2004) Prolonged diapause and the stability of host-parasitoid interactions. *Theoretical Population Biology* 65: 193–203. doi: 10.1016/j.tpb.2003.09.005
- Danforth BN (1999) Emergence dynamics and bet hedging in a desert bee, *Perdita portalis*. *Proceedings of the Royal Society B* 266: 1985–1994. doi: 10.1098/rspb.1999.0876
- Danks HV (1987) *Insect Dormancy: An Ecological Perspective*. Biological Survey of Canada, National Museum of Natural Science, Ottawa, 439 pp.
- Denlinger DL (2002) Regulation of Diapause. *Annual Review of Entomology* 47: 93–122. doi: 10.1146/annurev.ento.47.091201.145137
- Dupuis JR, Sperling FAH (2015) Repeated reticulate evolution in North American *Papilio machaon* group swallowtail butterflies. *PLOS ONE* 10: e0141882. doi: 10.1371/journal.pone.0141882
- Dupuis JR, Sperling FAH (in review) Hybrid dynamics in a species group of swallowtail butterflies. *The Journal of Evolutionary Biology*.
- Eliopoulos PA, Stathas GJ (2003) Temperature-dependent development of the koinobiont endoparasitoid *Venturia canescens* (Gravenhorst) (Hymenoptera: Ichneumonidae): effect of host instar. *Environmental Entomology* 32: 1049–1055. doi: 10.1603/0046-225X-32.5.1049
- Griffiths KJ (1969) Development and diapause in *Pleolophus basizonus* (Hymenoptera: Ichneumonidae). *The Canadian Entomologist* 101: 907–914. doi: 10.4039/Ent101907-9
- Hanski I (1988) Four kinds of extra long diapause in insects: a review of theory and observations. *Annales Zoologici Fennici* 25: 37–53.
- Heinrich GH (1962) Synopsis of Nearctic Ichneumoninae Stenopneusticae with particular reference to the northeastern region (Hymenoptera). VI. *Canadian Entomologist Supplement* 27: 677–802.

- Hopper KR (1999) Risk-spreading and bet-hedging in insect population biology. Annual Review of Entomology 44: 535–560. doi: 10.1146/annurev.ento.44.1.535
- Ivanov MF, Reznik SY (2008) Photoperiodic regulation of the diapause of the progeny in *Trichogramma embryophagum* Htg. (Hymenoptera, Trichogrammatidae): dynamics of sensitivity to photoperiod at the immature stages of maternal females. Entomological Review 88: 261–268. doi: 10.1134/S0013873808030019
- Laing JE, Corrigan JE (1995) Diapause induction and post-diapause emergence in *Trichogramma minutum* Riley (Hymenoptera: Trichogrammatidae): the role of host species, temperature, and photoperiod. The Canadian Entomologist 127: 103–110. doi: 10.4039/Ent127103-1
- LaSalle J, Gauld ID (1993) Hymenoptera and Biodiversity. CAB International, Wallingford, 348 pp.
- Martinek V (1985) Egg- and larval parasites of the European pine sawfly *Neodiprion sertifer* (GEOFF.) in Bohemia. Academia, nakl. Československé akademie věd 1: 1–123.
- Menu F, Debouzie D (1993) Coin-flipping plasticity and prolonged diapause in insects: example of the chestnut weevil *Curculio elephas* (Coleoptera: Curculionidae). Oecologia 93: 367–373. doi: 10.1007/BF00317880
- Oliver CG (1969) Experiments on the diapause dynamics of *Papilio polyxenes*. Journal of Insect Physiology 15: 1479–1589. doi: 10.1016/0022-1910(69)90178-4
- Prota R (1962) Note morfo-etologiche su *Trogus violaceus* (Mocs) (Hymenoptera: Ichneumonidae), endoparassita solitario delle larve di *Papilio hospiton* Génè (Lepidoptera, Papilionidae). Bolletino Istituto di Entomologia, Università Bologna 26: 289–213.
- R Core Team (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>
- Ringel MS, Rees M, Godfray HCJ (1998) The evolution of diapause in a coupled host-parasitoid system. Journal of Theoretical Biology 194: 195–204. doi: 10.1006/jtbi.1998.0754
- Scott JA (1986) The butterflies of North America: a natural history and field guide. Stanford University Press, Stanford, California, 584 pp.
- Shaw MR, Kan P, Kan-van Limburg Stirum B (2015) Emergence behaviour of adult *Trogus lapidator* (Fabricius) (Hymenoptera, Ichneumonidae, Ichneumoninae, Heresiarchini) from pupa of its host *Papilio machaon* L. (Lepidoptera, Papilionidae), with a comparative overview of emergence of Ichneumonidae from Lepidoptera pupae in Europe. Journal of Hymenoptera Research 47: 65–85. doi: 10.3897/JHR.47.6508
- Shimada K (1983) Photoperiodic induction of diapause in normal and allatectomized precocious pupae of *Papilio machaon*. Journal of Insect Physiology 29: 801–806. doi: 10.1016/0022-1910(83)90010-0
- Sime KR (2005) The natural history of the parasitic wasp *Trogus pennator* (Hymenoptera: Ichneumonidae): host-finding behaviour and a possible host countermeasure. Journal of Natural History 39: 1367–1380. doi: 10.1080/00222930400004370
- Sime KR, Wahl DB (2002) The cladistics and biology of the *Callajoppa* genus-group (Hymenoptera: Ichneumonidae, Ichneumoninae). Zoological Journal of the Linnean Society 134: 1–56. doi: 10.1046/j.1096-3642.2002.00006.x
- Sims SR (1980) Diapause dynamics and host plant suitability of *Papilio zelicaon* (Lepidoptera: Papilionidae). The American Midland Naturalist 103: 375–384. doi: 10.2307/2424637

- Sims SR (2007) Diapause dynamics, seasonal phenology, and pupal color dimorphism of *Papilio polyxenes* in southern Florida, USA. *Entomologia Experimentalis et Applicata* 123: 239–245. doi: 10.1111/j.1570-7458.2007.00552.x
- Soula D, Menu F (2005) Extended life cycle in the chestnut weevil: prolonged or repeated diapause? *Entomologia Experimentalis et Applicata* 115: 333–340. doi: 10.1111/j.1570-7458.2005.00281.x
- Sperling FAH (1986) Evolution of the *Papilio machaon* species group in western Canada (Lepidoptera: Papilionidae). MSc Thesis. University of Alberta, Edmonton, Alberta, Canada.
- Sperling FAH (1987) Evolution of the *Papilio machaon* species group in western Canada (Lepidoptera: Papilionidae). *Quaestiones Entomologicae* 23: 198–315.
- Sperling FAH (1990) Interspecific hybrids in *Papilio* butterflies: Poor taxonomy or interesting evolutionary problem? *Canadian Journal of Zoology* 68: 1790–1799. doi: 10.1139/z90-260
- Tauber MJ, Tauber CA, Masaki S (1986) *Seasonal Adaptations of Insects*. Oxford University Press, Oxford, 411 pp.
- Wahl DB, Sime KR (2006) A revision of the genus *Trogus* (Hymenoptera: Ichneumonidae, Ichneumoninae). *Systematic Entomology* 31: 584–610. doi: 10.1111/j.1365-3113.2006.00329.x
- Wallner WE (1987) Factors affecting insect population dynamics: differences between outbreak and non-outbreak species. *Annual Review of Entomology* 32: 317–340. doi: 10.1146/annurev.en.32.010187.001533