

FORUM

Phenotypic Plasticity and Fitness in Egg Parasitoids

GUY BOIVIN

Horticultural Research and Development Centre, Agriculture and Agri-Food Canada, 430 Boulevard Gouin, St-Jean-sur-Richelieu, Qc, J3B 3E6 Canada; Department of Natural Resource Sciences (Entomology), Macdonald Campus of McGill Univ, 2111 Lakeshore Road, Ste-Anne-de-Bellevue, Qc, H9X 3V9 Canada

Edited by Fernando L Consoli – ESALQ/USP

Neotropical Entomology 39(4):457-463 (2010)

ABSTRACT - Several proxies can be used to estimate the fitness of egg parasitoids: size, longevity, fecundity, mating ability and vagility. All these proxies are positively correlated with the lifetime fitness gain of an individual. However, the phenotypic plasticity, which is the ability of a genotype to produce distinct phenotypes depending on environmental conditions, may alter the value of these proxies. Host related factors (host species and quality), competition and duration of development will influence the proxies expressed by a given phenotype. When the phenotype is modified by the temperature at which an individual develops, the resulting phenotype will vary based on the life history strategy of the parasitoid. While in koinobiont species an increase in size is positively correlated with longevity and fecundity, the reverse occurs with idiobiont parasitoids. Using size as a proxy could thus be misleading depending on the factors that influence the size of the adult.

KEY WORDS: Fitness, proxy, reproduction, longevity, phenotype

Most optimality models are based on the assumption that organisms optimize some physiological or behavioral characteristics in order to maximize their lifetime fitness (Stephens & Krebs 1986). Fitness, defined here as the success of an individual in passing on copies of its genes to future generations (Bolhuis & Giraldeau 2005), is therefore used as a measure of success and any change in the morphology, physiology or behavior of an animal that increases its lifetime fitness is expected to be positively selected. This concept is central in behavioral ecology and both direct fitness and inclusive fitness are recognized. Direct fitness refers to the fitness gained by an individual through the production of its own offspring while inclusive fitness refers to the sum of the direct fitness plus the indirect fitness gained by the reproduction of nondescendant relatives (Krebs & Davies 1997).

Insect parasitoids are good organisms to test hypothesis in behavioral ecology as the expression of behaviors associated with host localization and parasitization are directly linked to a gain in fitness. Indeed, finding and successfully parasitizing a host results in additional progeny and therefore in an increase in fitness (Godfray 1994). Another research area where measures of fitness are used for parasitoids is applied ecology and in particular biological control (Roitberg *et al* 2001). When comparing different species or genotypes within a species for their potential in biological control programs, measures of fitness can be used to assess their capacity to multiply and control a targeted pest.

However, measuring directly fitness is a difficult and time-consuming process. One would have to measure the relative performance of genotypes and quantify their representation

in a population over several generations (Hoffman 1994). In general, proxies that give absolute values, such as size, longevity, fecundity etc., are used to approximate the fitness of an individual. The different proxies that can be used for parasitoids along with their advantages and limitations have been discussed by Roitberg *et al* (2001). In this paper I would like to concentrate on egg parasitoids and discuss how the phenotypic plasticity found in these organisms influences their fitness.

Egg Parasitoids

Egg parasitoids are found in several Hymenoptera families (Trichogrammatidae, Mymaridae, Eulophidae, Scelionidae, Aphelinidae and Encyrtidae) but most of the information available on egg parasitoids comes from the few families used in biological control. This is a polyphyletic group that has in common the complete immature development occurring inside the host egg. This group faces major constraints that influence which proxies should be used to measure their fitness and what are the limits of these proxies. Obviously, egg parasitoids are small, most of them being barely 1 mm long. In fact, the smallest insect known is a Mymaridae, *Dicopomorpha echmepterygis* Mockford, that parasitizes eggs of Psocoptera and whose males measure 140 µm (Mockford 1997, Gahlhoff 1998). Such a small size imposes strict limits to the capacity of these insects to disperse directionally and to the quantity of resources they can store. Not surprisingly they also display a very short lifespan, in the range of several hours to a few days. While

these characteristics result in difficulties when it comes to use these insects in laboratory tests, they also open opportunities such as measuring the lifetime fecundity of females in less than a week.

Another characteristic of egg parasitoids is that most species display structured populations and often intense sib-mating at the emergence site, although some off-patch mating occurs (Martel & Boivin 2007). Such mating structure influences the relative importance of dispersion and insemination capacity of males in their estimation of fitness.

Which Proxies Are Valid in Egg Parasitoids?

Roitberg *et al* (2001) have identified ten fitness proxies of importance for parasitoids. Of these, five are especially relevant for egg parasitoids: size, longevity, fecundity, mating ability and vagility. The other proxies proposed by Roitberg *et al* (2001) also apply to egg parasitoids, but in most cases the biology or ecology of egg parasitoids make them poor proxies for fitness. These poor proxies are: 1) Progeny survival is certainly important for larval and pupal parasitoids where the host immune system must be overcome or where hyperparasitoids are a major source of mortality. In egg parasitoids neither occur and only mortality due to competition following superparasitism could occur; 2) Developmental rate has an impact on the population dynamics of most parasitoid species. However, the development of most egg parasitoid species lasts 8 to 10 days and the observed variability in emergence is rather low (Doyon & Boivin 2006); 3) Sex ratio is considered as a weighting proxy when used in conjunction with realised fecundity, but it has no value as an absolute measure (Roitberg *et al* 2001); 4) Host acquisition measures the ability to find, overcome and parasitize hosts. Because host eggs are immobile and defenceless, unless defended by the ovipositing female as in several species of Scelionidae (Waage 1982), vagility is more important as a measure of the capacity of egg parasitoids to find and parasitize hosts; 5) Finally, oviposition propensity measures the tendency to accept hosts (Bourchier & Smith 1996). It is difficult to measure and is linked to host preference.

The Proxies Adapted to Egg Parasitoids

Size is considered as a good indicator of fitness although it has no direct relation with fitness. However, most other proxies are influenced by the size of an individual and in most cases a positive relationship is found (West *et al* 1996, Nicol & Mackauer 1999) (but see the section on phenotypic variability). In several species of *Trichogramma*, size was found to be positively correlated with the number of oocytes at emergence, progeny produced over 24h, searching activity, host and female encounter rates for females and males respectively (Boldt 1974, Bai *et al* 1992, Kazmer & Luck 1995, Boivin & Lagacé 1999).

Longevity is critical for egg parasitoids especially when it comes to finding host patches. Most egg parasitoids are poor

disperser and meteorological conditions such as wind, rain or solar radiation influence the capacity of these organisms to disperse to find hosts (Fournier & Boivin 2000, Fatouros *et al* 2008). Some species even respond to changes in barometric pressure by decreasing their propensity to fly (Fournier *et al* 2005). Individuals with a longer life expectancy can survive unfavorable conditions and find hosts afterward. The life expectancy of an individual also modifies its patch exploitation strategy (Wajnberg *et al* 2006).

Fecundity is probably the most important fitness proxy for female egg parasitoids. In numerous egg parasitoid species, a single host egg mass may be sufficient for a female to deposit all her egg load and a reduced fecundity will translate in lost opportunities and therefore decreased fitness. The temporal distribution of investment in reproduction in female parasitoids is described by the ovigeny index (Jervis *et al* 2001). Pro-ovigenic species have all their egg complement mature upon emergence, while synovigenic species have no mature egg at emergence and mature them during their life. Most species of egg parasitoids are either pro-ovigenic or moderately synovigenic, and a large proportion of the potential fecundity of a female is present at emergence (Jervis *et al* 2001). The potential fecundity at emergence is therefore a good fitness proxy for these species.

Mating ability is the most important proxy for male egg parasitoids. The sex ratio at the emergence patch is normally strongly females-biased and the males have access to numerous females soon after emergence. The reproduction investment in male parasitoids is described by the spermatogenic index (Boivin *et al* 2005). Males of *Trichogramma* species are prospermatogenic (Boivin *et al* 2005, Damiens & Boivin 2005), males emerge with their full sperm complement and do not produce more in their adult life. In the Mymaridae *Anaphes victus* Huber, males are moderately synspermatogenic, having an ovigeny index of 0.27 (G Boivin, unpublished data). In species with prospermatogenic males, any increase in the number of sperm present at emergence could enable the male to mate more females if they are present, either on the emergence patch or on another patch.

Vagility is important both for males and females. In males, since off-patch mating occurs (Martel & Boivin 2007), the capacity to disperse to another patch containing females is essential once all females on the emergence patch have been inseminated. Any increase in sperm production could only be expressed if the male has the capacity to disperse. For females, vagility influences their capacity to disperse in search of hosts (Bourchier & Smith 1996, Bennett & Hoffmann 1998, Romeis *et al* 2005). Factors such as wing size and shape influence the capacity of *Trichogramma* females to disperse and therefore affect directly their fitness through their capacity to find and parasitize hosts (Kölliker-Ott *et al* 2003).

Phenotypic Plasticity

All the factors previously mentioned act on the fitness gain of an individual. Any individual with characteristics that are favorable under the set of conditions it encounters will

leave more progeny and therefore gain more fitness. This selection acts on the genotypic variability that is observed for the proxies within a population. Several studies have looked at genetic variation in life history and behavioral traits of parasitoids (Carton *et al* 1989, Cronin & Strong 1996). For example, a female with a better vagility will have more chances of finding hosts and will be able to express her full potential fecundity (Kölliker-Ott *et al* 2003, 2004).

Another factor acts on the fitness proxies. Within a genotype, phenotypic plasticity occurs when the expression of a trait changes with the environment in which the organism is raised (Roff 1992). Phenotypic plasticity is thus the ability of a genotype to produce distinct phenotypes by altering its physiology, morphology, or development in response to changes in the environment (Pigliucci 2005, Colinet *et al* 2007). Thus, within the same genotype, different individuals will show fitness proxies that differ based on the conditions under which they developed. Selection will act on the genotype via the expressed phenotype and in a sense will act on the choices made by a female when allocating its progeny to different hosts or habitats. A genotype that expresses phenotypic plasticity in response to external conditions is therefore expected to have a selective advantage in a given condition (Zhivotovsky *et al* 1996, Moreno-Garcia *et al* 2010).

Phenotypic plasticity is a major factor in insect parasitoids. For example, the size of adult parasitoids depends on the quality of the host in or on which they developed (Godfray 1994). Siblings that develop in different hosts may express phenotypes that are very different. We will see later which factors influence host quality and therefore the expressed phenotype of the adult parasitoid. Such phenotypic plasticity has been demonstrated in several species of egg parasitoids (Olson & Andow 2002) and we expect the fitness of egg parasitoids to be strongly influenced by the factors acting on the phenotypic plasticity.

In egg parasitoids, data support the presence of phenotypic plasticity in morphological and physiological characteristics along with aspects of behavior.

Morphology: size. Size is the most obvious effect of phenotypic plasticity on egg parasitoids. Adults vary in their size based on the host species in which they developed from, the level of superparasitism and factors such as age of the host egg at the time of oviposition. Variation can reach 32-fold in the Pteromalidae *Nasonia vitripennis* (Walker) (O'Neill & Skinner 1990). Wing length can vary by 36% in the Mymaridae *Anaphes nitens* Girault when reared on eggs of the snout beetle *Gonipterus scutellatus* Gyll. (Santolamazza-Carbone *et al* 2007) and tibia length decreases by 13% in *A. victus* when females superparasitize host eggs parasitized seven days before (van Baaren *et al* 1995a). In *Trichogramma euproctidis* (Girault), female tibia length is 115 μm when they emerge singly from *Plutella xylostella* (L.), but increases to 196 μm when emerging singly from *Trichoplusia ni* (Hubner) eggs (V. Martel & G. Boivin, unpublished data). In general, variations in size due to host quality are positively correlated with other fitness proxies as mentioned before. However, when size differences originate from development at different temperatures, the relationship may be inversely correlated (see

section on duration of development).

Physiology: rate of development. Little information is available on the phenotypic plasticity of duration of development in egg parasitoids. Duration of development is obviously dependent on temperature, but even at the same temperature, the host species could influence the duration of the immature stage of egg parasitoids. In *T. euproctidis*, females that develop in eggs of *Plutella xylostella* emerge in average after 10.0 days when reared at 24°C, while females that develop singly in the larger eggs of *T. ni* emerge in average after 9.4 days (G. Boivin, unpublished data).

Physiology: fecundity of females. Fecundity in most insects varies with body size (Honek 1993) and, as expected, the size of female egg parasitoids has a positive effect on the number of oocytes (O'Neill & Skinner 1990). Lifetime fecundity has been reported to vary from 18 to 56 eggs in females of *T. euproctidis* that emerged from *P. xylostella* (head width 140 μm) and *Anagasta kuehniella* (Zeller) (head width 166 μm), respectively (Boivin & Lagacé 1999). In *Trichogramma brassicae* Bezdenko, *T. evanescens* Westwood and *T. cacoeciae* Marchal, lifetime fecundity increased by 25-30% when reared on *A. kuehniella* rather than in the smaller eggs of *Cadra cautella* (Walker) (Özder & Kara 2010). The effect of this parameter is likely to influence the number of progeny a female can have and therefore it will influence the selection occurring on the associated genotype. A positive correlation between body size and egg size has been reported in *Trichogramma* species (Klomp & Teerink 1966, G. Boivin unpublished data).

Physiology: number of sperm in males. An equivalent effect of size on the number of sperm in males is described (Henter 2004), but is not universal (Burton-Chellew *et al* 2007). In general large males have more sperm available on emergence than small males. This reduction in the number of sperm is definitive in prospermatogenic species whose males do not produce sperm during their adult live (Boivin *et al* 2005). However, even in partially synspermatogenic species, where males produce sperm during their adult life, small size could result in fewer sperm that can be stored in the seminal vesicles (Lacoume *et al* 2006). Obviously males that are limited in the number of sperm available will inseminate fewer females or only partially inseminate females they mate. This limitation will have an effect only in situation where mating opportunities exceed the sperm capacity of males. We expect such situation to occur as a proportion of *T. euproctidis* males, a prospermatogenic species (Damiens & Boivin 2005), that disperse from the emergence patch after mating is sperm-depleted (Martel & Boivin 2007).

The size of an individual could affect not only the number of gametes (oocytes or sperm) they can produce or carry, but also the size of these gametes. The fact that small females produce smaller eggs has been described in several egg parasitoid species (Arakawa *et al* 2004, Jervis *et al* 2008). A similar effect on the length of sperm has been described in the Hymenoptera *Bombus terrestris* (L.) (Baer *et al* 2003) and has recently been found in two egg parasitoid species, *T. euproctidis* and the Mymaridae *Anaphes listronoti* Huber (G. Boivin *et al* unpublished data).

Behavior: patch exploitation. Patch exploitation by female parasitoids integrates several behavioral mechanisms (Pierre *et al* 2003, Wajnberg 2006) and is also expected to show phenotypic plasticity. Size, through variation in vagility, walking speed, egg load etc., should influence both the duration of patch exploitation and the number of hosts parasitized. In *Aphidius rhopalosiph* De Stefani Perez, smaller females that developed at higher temperature showed a longer patch residence time than larger females (Le Lann 2009). In *Trichogramma nubilale* Ertle & Davis phenotypic plasticity was found for both percentage parasitism of European corn borer masses and secondary sex ratios (Olson & Andow 2002).

Factors Influencing Phenotypic Variability in Egg Parasitoids

Host species. Parasitoids show some phenotypic plasticity in their host choice (Vos & Vet 2004). Obviously, the size of the host in which an egg parasitoid develops influences the size of the emerging adult and therefore several of its life history traits including host fidelity (Henry *et al* 2010). The quality of the host could also influence the size of the emerging adult. Two host eggs of the same size but from different species could represent resources of different nutritive values. This factor is likely to be more important in generalist species exploiting different host species.

Host condition. The size of the host is not the only factor that could influence the fitness of the developing parasitoid. As the host embryo develops within the egg, resources are used and although egg parasitoids can recycle part of the transformed resources, some of it is lost. As a result, egg parasitoid immatures that develop in older eggs have fewer resources to use and old host eggs are generally less preferred by most Trichogrammatidae species (Godin & Boivin 2000). However, because the size of the host egg does not change markedly as it ages, adults emerging from old and young host eggs show only a 15% difference in size, but females emerging from old host eggs show a reduction in fecundity of 80% (G. Boivin, unpublished data).

Other factors acting on host egg quality could also influence the phenotypic plasticity of the developing parasitoid, but few data is available to support this (Jervis *et al* 2008). The quality of the food of the host adult is expected to modify the quality of the egg content and indirectly act on the developing egg parasitoid. When the Scelionidae *Telenomus podisi* Ashmead developed in eggs of the predatory pentatomid *Podisus maculiventris* (Say) that fed on caterpillar that developed on herbivore-resistant soybean, its overall reproductive capacities was negatively affected (Orr & Boethel 1986).

Duration of development. The phenotypic plasticity of egg parasitoid could also be influenced by the duration of their development. As in most poikilotherm species, duration of development is influenced by temperature, individuals developing at higher temperature develop faster than at low temperature. The rate of development influences the size of the

adult according to the Temperature-Size Rule (TSR) (Atkinson 1994, Angilletta *et al* 2004). The longer the development, the larger will be the adult at the end of its development. The TSR has been verified in several parasitoid species (Elliott *et al* 1995, Bazzocchi *et al* 2003, Colinet *et al* 2007) and the rate of development influenced negatively not only size, but also fecundity, lipid reserve and longevity (Colinet *et al* 2007). The mechanism behind the TSR is still debated (Angilletta *et al* 2004), the individuals developing at low temperature could grow larger either because they have access to resources for longer or their use of the resources could be more efficient at low temperature.

The application of TSR to idiobiont parasitoids, such as egg parasitoids, is more problematic. Once an egg parasitoid immature is within its host egg, the resources are fixed and the size of the egg chorion does not change. Nonetheless, in preliminary tests, we showed that *T. euproctidis* reared at 15°C were significantly larger than when reared at 30°C as predicted by the TSR (G. Boivin unpublished data). However, the other parameters measured showed the opposite trend. The adults reared at 30°C, even if smaller, had a longer lifespan and the females were more fecund. Because the resources were fixed, the increase in size found in individuals reared at low temperature could be compensated by a decrease in reserve that reflected in longevity and fecundity. On the other hand, selection experiments showed that over 15 generations, the temperature at which oviposition occurred changed the efficiency of female *Trichogramma pretiosum* Riley at low and high temperatures (Carrière & Boivin 2001).

These data on TSR on egg parasitoids stress the fact that a positive correlation between size and other life history traits should not be taken as granted.

Competition. In solitary species, when two or more larvae share a host, contest competition occurs and supplementary larvae are killed either by direct fight or through physiological suppression (Mackauer 1990, Carignan *et al* 1995). Superparasitism is generally avoided through host discrimination (Roitberg & Mangel 1988), a behavior not unique to Hymenoptera parasitoids (Royer *et al* 1999). In gregarious and facultative gregarious parasitoid species, resources within a host have to be shared through scramble competition. The less resources available per developing immature, the smaller will be the adults emerging from that host (van Baaren *et al* 1995b). Immatures of *Trichogramma* feed very rapidly at the beginning of their development and most of the host egg resources are consumed within 9h after hatching at 25°C (Wu *et al* 2000). When several *Trichogramma* larvae share a host egg, some will be consumed by other larvae while the others will reach the pupal stage. Depending of the outcome of the scramble competition, the size of the emerging *Trichogramma* can be quite variable (G. Boivin unpublished data).

This factor is probably the one influencing most the size of the immatures and emerging adult in egg parasitoids. When *Trichogramma australicum* Girault develops in eggs of *Corcyra cephalonica* (Stainton), the pupae length varies from 0.56 mm for pupae developing singly to 0.34 mm when three larvae shared the same host (Brenière 1965). Differences in size (total body length) ranged from 0.52 mm (solitary) to 0.34 mm (eight individuals per egg) in *Trichogramma poliae*

Nagaraja females (Ahmad *et al* 2002) while the hind tibia length of *T. evanescens* varied from 192 μm for solitary individuals to 142 μm (four individuals per host egg) in eggs of *Mamestra brassicae* (L.) (Grenier *et al* 2001). There is generally a positive relationship between the size of the adults and most of the other fitness proxies measured when the difference in size is caused by competition within the host egg.

Conclusion

Measuring fitness in egg parasitoids is important both in behavioral ecology and biological control studies. The value of an individual can vary tremendously within the same genotype and this phenotypic plasticity has to be taken into account when evaluating behavioral choices or the efficiency of egg parasitoids to control a pest population. While size is often used to assess the value of individuals, the use of this proxy can be misleading.

When the variability in size is caused by intraspecific competition within the host egg, a positive relationship is found between the size of the adult and its reproductive capacity. The slope of the relationship changes when the difference in size is due to the quality of the host egg. Females developing in old host eggs are only 15% smaller than those developing in young host eggs yet their fecundity is decreased by 85%. When the difference in size is due to difference in rearing temperature, the effect can even be reversed, larger individuals that developed at lower temperature show a lower fecundity and longevity than smaller individuals reared at higher temperature. The safest solution remains the measure of several fitness proxies to provide a true picture of the value of an individual.

Acknowledgments

This research was supported in part by a grant from the Natural Sciences and Engineering Research Council of Canada (NSERC).

References

- Ahmad M, Ahmad M I, Mishra R K, Sheel S K (2002) Superparasitism by *Trichogramma poliae* in the eggs of *Clostera cupreata* (Lepidoptera: Notodontidae) and its effect on offspring. *J Trop For Sci* 14: 61-70.
- Angilletta M J, Steury T D, Sears M W (2004) Temperature, growth rate, and body size in ectotherms: fitting pieces of a life-history puzzle. *Integr Comp Biol* 44: 498-509.
- Arakawa R, Miura M, Fujita M (2004) Effects of host species on the body size, fecundity, and longevity of *Trissolcus mitsukurii* (Hymenoptera: Scelionidae). A solitary egg parasitoid of stink bugs. *Appl Entomol Zool* 39: 177-181.
- Atkinson D (1994) Temperature and organism size – a biological law for ectotherms? *Adv Ecol Res* 25:1-58.
- Baer B, Schmid-Hempel, Hoeg J T, Boomsma J J (2003) Sperm length, sperm storage and mating system characteristics in bumblebees. *Ins Sociaux* 50: 101-108.
- Bai B, Luck R F, Forster L, Stephens B, Janssen J A M (1992) The effect of host size on quality attributes of the egg parasitoid, *Trichogramma pretiosum*. *Entomol Exp Appl* 64: 37-48.
- Bazzocchi G G, Lanzoni A, Burgio G, Fiacconi M R (2003) Effects of temperature and host on the pre-imaginal development of the parasitoid *Diglyphus isaea* (Hymenoptera: Eulophidae). *Biol Control* 26:74-82.
- Bennett D M, Hoffmann A A (1998) Effects of size and fluctuating asymmetry on field fitness of the parasitoid *Trichogramma carverae* (Hymenoptera: Trichogrammatidae). *J Anim Ecol* 67: 580-591.
- Boivin G, Jacob S, Damiens D (2005) Spermatogeny as a life-history index in parasitoid wasps. *Oecologia* 143: 198-202.
- Boivin G, Lagacé M (1999) Effet de la taille sur la fitness de *Trichogramma evanescens* (Hymenoptera: Trichogrammatidae). *Ann Soc Entomol Fr* 35: 371-378.
- Boldt P E (1974) Temperature, humidity, and host: effect on rate of search of *Trichogramma evanescens* and *T. minutum* auctt. (not Riley, 1871). *Ann Entomol Soc Am* 67: 706-708.
- Bolhuis J J, Giraldeau L A (Eds) (2005) The behavior of animals: mechanisms, function, and evolution. Blackwell Publishing, MA, 536p.
- Bourchier R S, Smith S M (1996) Influence of environmental conditions and parasitoid quality on field performance of *Trichogramma minutum*. *Entomol Exp Appl* 80: 461-468.
- Brenière J (1965) Les trichogrammes parasites de *Procerasacchariphagus* Boj. borer de la canne à sucre à Madagascar. Partie 2 Étude biologique de *Trichogramma australicum* Gir. *Entomophaga* 10: 99-117.
- Burton-Chellew M N, Sykes E M, Patterson S, Shuker D M, West S A (2007) The cost of mating and the relationship between body size and fitness in males of the parasitoid wasp *Nasonia vitripennis*. *Evol Ecol Res* 9: 921-934.
- Carignan S, Boivin G, Stewart R K (1995) Developmental biology and morphology of *Peristenus digoneutis* Loan (Hymenoptera: Braconidae: Euphorinae). *Biol Control* 5: 553-560.
- Carrière Y, Boivin G (2001) Constraints on the evolution of thermal sensitivity of foraging in *Trichogramma*: genetic trade-offs and plasticity in maternal selection. *Am Nat* 157: 570-581.
- Carton Y, Capy P, Nappi A J (1989) Genetic variability of host-parasite relationship traits: utilization of isofemale lines in a *Drosophila simulans* parasitic wasp. *Genet Sel Evol* 21: 437-446.
- Colinet H, Boivin G, Hance T (2007) Manipulation of parasitoid size using the temperature-size rule: fitness consequences. *Oecologia* 152: 425-433.
- Cronin J T, Strong D R (1996) Genetics of oviposition success of a thelytokous fairyfly parasitoid, *Anagrus delicatus*. *Heredity* 76: 43-54.

- Damiens D, Boivin G (2005) Male reproductive strategy in *Trichogramma evanescens*: sperm production and allocation to females. *Physiol Entomol* 30: 241-247.
- Doyon J, Boivin G (2006) Impact of the timing of male emergence on mating capacity of males in *Trichogramma evanescens* Westwood. *BioControl* 51: 703-713.
- Elliott N C, Burd J D, Kindler S D, Lee J H (1995) Temperature effects on development of three cereal aphid parasitoids (Hymenoptera: Aphididae). *Great Lakes Entomol* 28:199-204.
- Fatouros N E, Dicke M, Mumm R, Meiners T, Hilker M (2008) Foraging behavior of egg parasitoids exploiting chemical information. *Behav Ecol* 19: 677-689.
- Fournier F, Boivin G (2000) Comparative dispersal of *Trichogramma evanescens* and *Trichogramma pretiosum* (Hymenoptera: Trichogrammatidae) in relation to environmental conditions. *Environ Entomol* 29: 55-63.
- Fournier F, Pelletier D, Vigneault C, Goyette B, Boivin G (2005) Effect of barometric pressure on flight initiation by *Trichogramma pretiosum* and *Trichogramma evanescens* (Hymenoptera: Trichogrammatidae). *Environ Entomol* 34: 1534-1540.
- Gahlhoff J E (1998) Book of insect records. University of Florida Press. Retrieved from <http://ufbir.ifas.ufl.edu/chap38.htm> Accessed in 9 January 2008.
- Godfray H C J (1994) Parasitoids: behavioral and evolutionary ecology. Princeton University Press, Princeton, 475p.
- Godin C, Boivin G (2000) Effects of host age on parasitism and progeny allocation in Trichogrammatidae. *Entomol Exp Appl* 97: 149-160.
- Grenier S, Grille G, Basso C, Pintureau B (2001) Effects of the host species and the number of parasitoids per host on the size of some *Trichogramma* species (Hymenoptera: Trichogrammatidae). *Biocontr Sci Tech* 11: 21-26.
- Henry L M, May N, Acheampong S, Gillespie D R, Roitberg B D (2010) Host-adapted parasitoids in biological control: does source matter? *Ecol Appl* 20: 242-250.
- Henter H J (2004) Constrained sex allocation in a parasitoid due to variation in male quality. *J Evol Biol* 17: 886-896.
- Hoffman AA (1994) Genetic analysis of territoriality of *Drosophila melanogaster*, p.188-205 in Boake C (ed) Quantitative genetic studies of behavioral evolution. University of Chicago Press, IL, 400p.
- Honek A (1993) Intraspecific variation in body size and fecundity in insects: a general relationship. *Oikos* 66: 483-492.
- Jervis M A, Eilers J, Harvey J A (2008) Resource acquisition, allocation, and utilization in parasitoid reproductive strategies. *Annu Rev Entomol* 53: 361-385.
- Jervis M A, Heimpel G E, Ferns P N, Harvey J A, Kidd N A C (2001) Life-history strategies in parasitoid wasps: a comparative analysis of 'ovigeny'. *J Anim Ecol* 70: 442-458.
- Kazmer D J, Luck R F (1995) Field tests of the size-fitness hypothesis in the egg parasitoid. *Trichogramma pretiosum*. *Ecology* 76: 412-425.
- Klomp H, Teerink B J (1966) The significance of oviposition rates in the egg parasite, *Trichogramma embryophagum*. *Arch Neerl Zool* 17: 350-375.
- Kölliker-Ott U M, Bigler F, Hoffmann A A (2004) Field dispersal and host location of *Trichogramma brassicae* is influenced by wing size but not wing shape. *Biol Contr* 31: 1-10.
- Kölliker-Ott U M, Blows M W, Hoffmann A A (2003) Are wing size, wing shape and asymmetry related to field fitness of *Trichogramma* egg parasitoids? *Oikos* 100: 563-573.
- Krebs J R, Davies N B (1997) The evolution of behavioural ecology, p.3-12. In Krebs J R, Davies N B (eds) Behavioural ecology: an evolutionary approach. 4th edition. Blackwell Publishing, MA, 464p.
- Lacoume S, Bressac C, Chevrier C (2006) Effect of host size on male fitness in the parasitoid wasp *Dinarmus basalis*. *J Ins Physiol* 52: 249-254.
- Le Lann C (2009) Partage de la ressource au sein d'une guild: des histoires de vie, comportements et réactions à la température contrastés. PhD thesis, Université de Rennes 1, Rennes, 289p.
- Mackauer M (1990) Host discrimination and larval competition in solitary endoparasitoids, p.41-62. In Mackauer M, Ehler L E, Roland J (eds) Critical issues in biological control, Intercept, Andover, 330p.
- Martel V., Boivin G (2007) Unequal distribution of local mating opportunities in an egg parasitoid. *Ecol Entomol* 32: 393-398.
- Mockford E L (1997) A new species of *Dicopomorpha* (Hymenoptera: Mymaridae) with diminutive, apterous males. *Ann Entomol Soc Am* 90: 115-120.
- Moreno-Garcia M, Lanz-Mendoza H, Córdoba-Aguilar A (2010) Genetic variance and genotype-by-environment interaction of immune response in *Aedes aegypti* (Diptera: Culicidae). *J Med Entomol* 47: 111-120.
- Nicol C M Y, Mackauer M (1999) The scaling of body size and mass in a host-parasitoid association: influence of host species and stage. *Entomol Exp Appl* 90: 83-92
- Olson D M, Andow D A (2002) Inheritance of an oviposition behavior by an egg parasitoid. *Heredity* 88: 437-443.
- O'Neill K M, Skinner S W (1990) Ovarian size and number in relation to female size in five species of parasitoid wasps. *J Zool Lond* 220: 115-122.
- Orr D B, Boethel D J (1986) Influence of plant antibiosis through four trophic levels. *70: 242-249.*
- Özder N, Kara G (2010) Comparative biology and life table of *Trichogramma cacoeciae*, *T. brassicae* and *T. evanescens* (Hymenoptera: Trichogrammatidae) with *Ephestia kuehniella* and *Cadra cautella* (Lepidoptera: Pyralidae) as hosts at three constant temperatures. *Biocontr Sci Tech* 20: 245-255.
- Pierre J S, van Baaren J, Boivin G (2003) Patch leaving decisions rules in parasitoids: do they use sequential decisional sampling? *Behav Ecol Sociobiol* 54:147-155.

- Pigliucci M (2005) Evolution of phenotypic plasticity: where are we going now? *Tree* 20:481-486.
- Roitberg B D, Boivin G, Vet L E M (2001) Fitness, parasitoids, and biological control: an opinion. *Can Entomol* 133: 429-438.
- Roitberg B D, Mangel M (1988) On the evolutionary ecology of marking pheromones. *Evol Ecol* 2: 289-315.
- Roff D A (1992) The evolution of life histories: theory and analysis. Chapman & Hall, New York, 535p.
- Romeis J, Babendreier D, Wäckers F L, Shanower T G (2005) Habitat and plant specificity of *Trichogramma* egg parasitoids – underlying mechanisms and implications. *Basic Appl Ecol* 6: 215-236.
- Royer L, Fournet S, Brunel E, Boivin G (1999) Intra- and interspecific host discrimination by host-seeking larvae of coleopteran parasitoids. *Oecologia* 118: 59-68.
- Santolamazza-Carbone S, Nieto M P, Rivera A C (2007) Maternal size and age affect offspring sex ratio in the solitary egg parasitoid *Anaphes nitens*. *Entomol Exp Appl* 125: 23-32.
- Stephens D W, Krebs J R (1986) Foraging theory. Princeton University Press, Princeton, 247p.
- van Baaren J, Boivin G, Nénon J P (1995a) Intraspecific hyperparasitism in a primary hymenopteran parasitoid. *Behav Ecol Sociobiol* 36: 237-242.
- van Baaren J, Nénon J P, Boivin G (1995b) Comparison of oviposition behavior of a solitary and a gregarious parasitoid (Hymenoptera: Mymaridae). *J Ins Behav* 8: 671-686.
- Vos M, Vet L E M (2004) Geographic variation in host acceptance by an insect parasitoid: genotype versus experience. *Evol Ecol Res* 6: 1021-1035.
- Waage J K (1982) Sib-mating and sex ratio strategies in scelionid wasps. *Ecol Entomol* 7: 103-112.
- Wajnberg E (2006) Time allocation strategies in insect parasitoids: from ultimate predictions to proximate behavioral mechanisms. *Behav Ecol Sociobiol* 60: 589-611.
- Wajnberg E, Bernhard P, Hamelin F, Boivin G (2006) Optimal patch time allocation for time-limited foragers. *Behav Ecol Sociobiol* 60: 1-10.
- West S A, Flanagan K E, Godfray H C J (1996) The relationship between parasitoid size and fitness in the field, a study of *Achrysocharoides zwoelferi* (Hymenoptera: Eulophidae). *J Anim Ecol* 65: 631-639.
- Wu Z X, Cohen A C, Nordlund D A (2000) The feeding behavior of *Trichogramma brassicae*: new evidence for selective ingestion of solid food. *Entomol Exp Appl* 96: 1-8.
- Zhivotovsky L A, Feldman M W, Bergman A (1996) On the evolution of phenotypic plasticity in a spatially heterogeneous environment. *Evolution* 50: 547-558.

Received 28/VI/10. Accepted 01/VII/10.
