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Adaptations to different habitats in sexual and asexual populations of parasitoid wasps: a meta-analysis

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Background. Coexistence of sexual and asexual populations remains a key question in evolutionary ecology. We address the question how an asexual and a sexual form of the parasitoid*Venturia canescens* can coexist in southern Europe and test the hypothesis that both forms are adapted to different habitats within their area of distribution.

Methods. We present a meta-analysis of known adaptations to these habitats. Sexuals inhabit natural environments that are highly unpredictable, and where density of wasps and their hosts is low and patchily distributed. Asexuals instead are common in anthropic environments (*e.g.* grain stores) where host outbreaks offer periods when egg-load is the main constraint on reproductive output.

Results. Seeking consilience from the differences between multiple traits we found that sexuals invest more in longevity at the expense of egg-load, are more mobile, and display higher plasticity in response to thermal variability than asexual counterparts.

Discussion. Thus, each form has consistent multiple adaptations to the ecological circumstances in the contrasting environments.

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Running header: Adaptations in sexual and asexual wasps

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Keywords: Local adaptation / Maintenance of sex / Trade-offs / *Venturia canescens*

Abstract:

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Introduction

Populations of a species from different localities often are locally adapted in life history traits, behavior and physiology (Kraaijeveld & van Alphen, 1995a; 1995b; Seyahooei et al., 2011a; 2011b) but individuals of a species from the same locality tend to have similar traits, because sexual reproduction and recombination prevent the divergence of genotypes. On the one hand, in the same conditions, individuals that reproduce asexually become genetically isolated from the sexual members of the population and thus the sexually reproducing individuals and the asexually reproducing clones could accumulate genetic differences. On the other hand, when sexually reproducing individuals and asexual clones occupy the same niche, normalizing selection would prevent divergence by random drift between sexuals and asexuals.

A variety of processes, including "loss of sexuality" mutations, hybridization and endosymbiotic infection, cause the occasional generation of asexual strains from sexually reproducing individuals in a range of eukaryotic taxa (Butlin, 2002; Neiman et al., 2014; van der Kooi & Schwander, 2014). This phenomenon leads to competition between the newly created asexual strain and the ancestral sexual strain (Lively, 2010; Innes & Ginn, 2014). When both reproductive modes are obligatory and remain thereafter reproductively isolated, competitive interactions between them could favor individuals of one of the reproductive modes over the other. Asexual individuals, except for their reproductive mode, may differ little in phenotype from their sexual ancestors. Hence, which reproductive mode will be favored depends on the balance between the benefits and costs of sex. These costs result from the inefficiencies of sexual reproduction when compared to the asexual one (Maynard Smith, 1978; recently reviewed by Lehtonen et al., 2012; Meirmans et al., 2012, and Stelzer, 2015). If environmental conditions enable asexuals to fully express their reproductive advantages (*i.e.* the avoidance of mating and of production of male

offspring), this mode of reproduction is superior and will replace the sexual form (Maynard Smith, 1978).

Theoretical studies reveal that coexistence of sexual and asexual competitors is only possible if the newly arisen asexual forms have a smaller inhibitory effect on the sexual forms than the sexual strains have on themselves (Case & Taper, 1986; Gaggiotti, 1994; Doncaster et al., 2000). For instance, coexistence at the geographical level is favored if the habitat is structured as a mosaic of environments in which either one or the other form performs better (Tilquin & Kokko, 2016). Asexually reproducing forms are expected to bloom in environments where conditions provide opportunities for reproduction at the maximum possible rate, and conditions affecting survival are benign and stable. Sexual forms may resist asexual invasion in environments that are more temporally or spatially heterogeneous, thanks to their higher genetic diversity (Park et al., 2014). Over time each form could develop further adaptations to match its preferred environment.

Empirical tests of this theory are lacking (see Letho & Haag, 2010). Such a test would require (1) a demonstration that the sexually reproducing form differs in habitat use from the a-sexual form, (2) evidence that the habitat used by the a-sexually reproducing clones is more benign and / or stable in space and time than that of the sexually reproducing form, regarding factors affecting survival and (3) that individuals of both reproductive modes are adapted in behavior, physiology and life history traits to their respective habitats.

We test the theory bringing together different strands of research in a hymenopteran parasitoid that fits the scenario introduced above. Transitions from sexual reproduction to asexuality have occurred repeatedly and independently in hymenopteran parasitoids (Godfray, 1994; van Wilgenburg et al., 2006; Heimpel & de Boer, 2008). In these insects, adaptation to different environments is tightly constrained by three main trade-offs (Jervis et al., 2007; 2008;

Segoli & Rosenheim, 2013): 1- allocation to soma (mainly exoskeleton and musculature) versus non-soma (reproductive tissues and gametes, together with initial nutrient reserves); 2- allocation to teneral egg complement versus initial reserves, which is an expression of the classical trade-off between immediate reproduction and survival (for future reproduction); and 3- allocation of resources not assigned to reproduction to either survival or locomotion. The resolution of these trade-offs in different environments should lead to different patterns of adaptation in life-history, as observed, for instance, among populations of *Asobara tabida* (Kraaijeveld & van Alphen, 1995a; 1995b) and *Leptopilina boulardi* (Moiroux et al., 2010; Seyahooei et al., 2011a; 2011b) or in hyperparasitoids *Gelis* spp. (Visser et al., 2016), but also in behaviors and morphology.

This work aims, through a meta-analysis of life history traits involved in the above mentioned trade-offs, of foraging behavior and morphology to provide an empirical test of the theory outlined above using the parasitoid *Venturia canescens* G. (*Hymenoptera: Ichneumonidae*).

We chose *V. canescens* for four reasons. First, both reproductive modes are obligatory (*i.e.* there is no cyclic asexuality) with no known direct benefit of sex such as the formation of resting stages (Beukeboom et al., 1999). Second, it is one of the few hymenoptera species where obligated sexual and asexual individuals co-occur and where asexuality is not caused by bacterial endosymbionts (Beukeboom & Pijnacker 2000; Mateo Leach et al., 2009; Foray et al., 2013b). This characteristic allows us to focus on the ecological factors that impinge on the persistence of both forms independently of the coevolution of the system host-symbionts (Duron et al., 2008; Werren et al., 2008; Ma et al., 2014). Third, no genetic exchanges through matings occur in natural populations between reproductive modes (Mateo-Leach et al., 2012), preserving different genetic entities and allowing ecological differences. The fourth reason to focus on *V. canescens* is the large number of studies published in the last 17 years providing a wealth of data on the life history and

foraging behavior of asexual and sexual forms (Table 1). These studies allow a rich set of comparisons, which have not as yet been exploited to test the pattern of adaptation of each form to its preferential environment (see Meirmans et al., 2012 for a qualitative discussion of some traits). Each of the studies included in our analysis examines a behavioral response in either strain under specific conditions (e.g. exploitation of hosts under changing weather conditions, Amat et al., 2006), or a life-history-trait. The combination of data on a large number of life history and behavioral traits allows us to depict how changes in a whole suit of traits have resulted in adaptation of wasps both reproductive modes to their respective habitats. Also, our meta-analysis allows assessing the relative contribution of physiological and behavioral traits and trade-offs to adaption in different environments.

Our predictions can be summarized as follows:

Life history trade-offs: We expect differences in egg load, survival and flight capability between both forms of *V. canescens* due to the trade-off between current and future reproduction. In natural habitats the majority of individuals are sexuals (asexuals are occasionally found (Schneider et al., 2002; Amat, 2004) but their origin is unknown) exploiting sparsely distributed hosts (Driessen & Bernstein, 1999). This should favor a higher investment in survival and flight capability for future reproduction at the cost of lower egg production, because egg availability is not the main constraint in reproductive output, in comparison to asexuals. The latter live in grain stores and mills, where host distribution is aggregated (Bowditch & Madden 1996) and the amplitude of host density variations is very large (Campbell & Arbogast, 2004; Arbogast et al., 2005a; Arbogast et al., 2005b; Belda & Riudavets, 2013). These environmental conditions should favor higher investment in the production of eggs available for immediate reproduction, with respect to survival and flight capability. This is consistent with theoretical considerations that indicate that heterogeneous

distribution of hosts through time and space promotes higher egg production at the expense of other life history traits (Ellers et al., 2000). When finding patches with high host density, animals with higher egg loads could disproportionally contribute to future generations.

Behavior: Response to weather conditions: Environmental cues for forthcoming weather changes, such as sudden drops in temperature or atmospheric pressure can be exploited to adjust foraging or laying behavior, and sensitivity to such cues should be most favored when weather conditions are more unstable, as occurs between natural and storage habitats. For instance, predictable higher mortality during bad weather should promote exploiting host-patches more thoroughly than otherwise (e.g. staying longer or laying more eggs; Mangel, 1989; Roitberg et al., 1992; Roitberg et al., 1993; Sirot et al., 1997). On this basis, we expect wasps adapted to field conditions to be more sensitive to weather parameters than those from mills and stores.

Behavior: Response to intraspecific competition: Female parasitoids compete by superparasitism, *i.e.* by laying eggs in already parasitized hosts. As this often results in the death of supernumerary larvae (van Alphen and Visser 1990), fitness returns of oviposition in parasitized hosts are often lower than of ovipositions in unparasitized hosts. Most parasitoid species mark their hosts with chemicals that inform other females that the host is already parasitized (van Lenteren, 1981; Marris et al., 1996; Nufio & Papaj, 2001). Thus, females have the information to decide whether or not to lay in an already parasitized host. In natural environments the encounter rate with hosts is much lower than in grain stores and mills. Hence, sexual wasps should accept parasitized hosts more easily than asexuals.

Methods

Biological model:

Sexual reproduction in *V. canescens* follows the classical haplo-diploid mechanism of hymenopterans (arrhenotoky): males arise from unfertilized eggs and are haploid, while females originate from fertilized eggs and are diploid. Individuals born through this form of reproduction can be found in natural and semi-natural habitats (e.g. orchards), in the Mediterranean basin, where they can easily be attracted to baits containing the larvae of *Ephestia kuehniella* (Lepidoptera: pyralidae). The list of host species of *V. canescens* (Salt, 1976) includes *Ectomyelois ceratoniae* found in the wild in carob pods, Japanese medlars, and almonds, a common host in field studies (Driessen & Bernstein, 1999). In field conditions, food sources (sugar-rich substances such as nectar or exudates from fruits) are sufficiently available to allow *V. canescens* females to maintain a nearly constant energetic level (Casas et al., 2003; Desouhant et al., 2010).

In contrast, asexual *V. canescens* individuals are produced by automictic thelythoky, a genetically based thelytoky in which meiosis and crossing over occur prior to the restoration of diploidy through the fusion of two pronuclei or of two cleavage nuclei (Beukeboom and Pijnacker 2000). Asexually reproducing *V. canescens* are found throughout Europe and North America (Johnson et al., 2000; Schneider et al., 2002) mainly inside buildings and in association with stored products infested with *E. kuehniella*, *E. cautella* (Bowditch & Madden 1996) or *Plodia interpunctella* (Roesli et al., 2003, Campbell & Arbogast, 2004). Food for adults is rarely found in these environments (C. Bernstein, pers. obs.).

Overview and selection of the literature

The database for the meta-analysis was constituted by using ISI Web of Science (Web of Science Core Collection). We first selected all the papers with the topics "*Venturia canescens*". Among these papers we selected those with [(thelytok* AND arrhenotok*) OR (sex* AND asex*)] between 1999 (date of the first publication of the sexual *Venturia canescens;* Beukeboom et al.,

1999) and 2017 (February 10th). Thus, 22 studies, in which different characteristics of asexual and sexual individuals were compared in the laboratory or in the field, were retained (Fig. 1). Then we set apart genetic studies (n= 6) from life-history and behavioral studies (n= 16 encompassing 46 traits compared), and focused our analysis on these 16 studies (Tables 1 and 2). Most of the results from the genetic papers are treated in our introduction. We also included unpublished results of one doctoral dissertation (Amat, 2004) (see Fig.1). While addressed in the discussion, some results were not included in our meta–analysis; the reasons for each exclusion (in general for statistical arguments) are given in Supplementary Materials (Table 2).

To assist in reading and interpretation of the data, we segmented the different measures in 8 categories: size, 3 life history traits (fecundity, longevity, and energy level), 3 behavioral traits (flight, competition with conspecifics (superparasitism) and feeding), and one study of the capacity to respond to changes in temperature. In each category, several traits are considered and for each of these traits, from one to six measures from independent studies (henceforth referred as point) are provided.

Overview of statistical analyses

To compare the differences between the two forms for different traits, which by necessity are expressed in different units and have different ranges of variation, we transformed the results to dimensionless (standardized) *d* effect size measurements (Cohen 1988; Nakagawa and Cuthill 2007). *d* is devoid of units and thus comparable in a meta-analysis approach. Cohen (1988) suggested that *d* values of 0.2, 0.5 and 0.8 could be considered as corresponding to "small", "medium" and "large" biological effects, respectively. Effect sizes are given together with their 95% confidence intervals. Details of *d* calculations are presented in the Appendix A. Positive *d* values correspond to cases where sexuals invest more than asexuals in a category. For

198 superparasitism positive values would imply higher avoidance of hosts already parasitized by
199 sexuals and modification of patch residence time in response to these encounters by the same.

200

201 **Results**

202 We present the available comparisons in terms of *d* in Figure 1, and discuss the traits of each
203 category individually below, identifying trait measurement by the number of the entry in figure 1.

204 Figure 1 shows medium to very large effects sizes (meaning large biological differences
205 between forms) for traits likely to affect fecundity. Egg load (points 1-4), number of ovarioles
206 (point 5) and ability to find hosts (at a short distance by walking in an olfactometer, points 6 and
207 8) are all greater in the asexual form. Asexual females are larger than sexual ones even when both
208 are reared in the same host species (points 10-15).

209 The large effect size for point 50 shows that longevity is higher in sexual than asexual *V.*
210 *canescens*. Pelosse et al., (2010) also reported higher longevity in sexual individuals (point 48) but
211 their confidence intervals included the possibility of lack of effect. Barke et al., (2005) considered
212 the difference in longevity between sexual and asexual forms under different temperatures and
213 different levels of food availability. They did not find differences between unfed animals of both
214 forms, but when wasps were fed, sexuals had higher longevity. The results for 15°C are significant
215 but the data provided do not allow calculating a *d* value. Points 49 and 47 show the *d* values for
216 25°C and 29 °C. The confidence intervals for the latter show a lack of effect. On the whole, these
217 data show higher longevity of sexual than asexual forms.

218 The studies of Foray et al., (2011), Pelosse et al., (2010) and Barke et al., (2005) treated
219 egg load and longevity as independent traits, but the two traits cannot be jointly maximized. The

resolution to the resulting trade-off differs between forms: asexuals invest preferentially in fecundity at the cost of life expectancy, and the opposite occurs in sexual wasps (Pelosse et al., 2007). How this translates in lifetime reproductive success depends on the environment. In the experimental conditions used by Barke et al., (2005) akin to indoor situations, sexual forms produced a greater lifetime number of offspring (point 44). This result seems unexpected but under their experimental conditions honey-fed wasps do not need much energy for flying and they can reallocate this energy to fecundity as they are partly synovigenic (*i.e.* able to mature eggs during their whole lifetime). Moreover advantage of asexuals in terms of fecundity remains since daughter production by sexual females is lower than by asexual ones. Indeed even if the offspring sex ratio was not recorded in this study, Metzger et al., (2008) and Beukeboom (2001) showed a balanced or a slightly biased sex ratio towards females in *V. canescens*.

As the scarcity of hosts in the field requires frequent and long flights, sexual *V. canescens* should benefit from a higher investment in flying capacity than their asexual counterparts. This higher investment has been indeed observed under experimental conditions (in the field and in lab), as evidenced by the small to large effect sizes of the traits belonging to flight category (except for the null *d* values obtained for total distance flown and total time in flight during the experiment, points 19 and 20). Flight measurements deserve some unpacking. As recorded, flight bouts were composed by an alternation of periods actually flying and resting. What was observed was that sexual wasps covered similar distances in fewer flights (lower number of stop, trait 34). Sexual wasps fly faster (points 35, 38 and 39).

Flight is a particularly energy-demanding behavior (Harrison and Roberts 2000) that in *V. canescens* and other insects depends mostly on the consumption of glycogen (Amat et al., 2012). Consistently with their greater dependence on flight, sexual females have higher total metabolic

reserves at emergence than asexual ones (point 41). Interestingly, the amount of nutrients not involved in flight show small *d* values (non-significantly different from 0; proteins: point 25; lipids: points 29 and 28; glucose: point 23 and 24, and free carbohydrates: point 26), but effect size for glycogen reserves are medium to high, with greater glycogen contents in sexual than asexual females (points 51-53). The consumption rates of glycogen (consumption per unit time) do not differ between modes of reproduction (point 27). The results of field experiments are consistent with differences in behavioral and physiological traits found in the laboratory: sexual *V. canescens* initiate dispersal faster after release (point 37) and are less often recaptured in the vicinity of the release point (point 33). Although this could be attributed to the traps being less attractive to sexuals at distance, the result is also consistent with sexuals being more mobile and leaving earlier the release site.

Difference in initial energy reserves between adults of the two forms can potentially be compensated by feeding on carbohydrates. When experimentally offered food, asexuals have the same feeding behavior as sexual forms (feeding time and number of feeding bouts per unit of observation time) (points 46 and 9) However, there is more food available in the field than in stores.

Response to weather conditions:

Sexual, but not asexual, individuals respond to a sudden drop in temperature by exploiting each host-patch more thoroughly (e.g. laying more eggs (point 42), and staying longer). This is consistent with the predicted difference in sensitivity to weather cues. The faster recovering of sexuals from chill coma (point 40) is also indicative of sexuals' higher capability to deal with temperature changes. The higher responsiveness of sexual individuals to temperature changes is also reflected by the large positive *d* value in point 55. This point illustrates the higher breadth of

sexual performance (quantified by maximal egg load) curve when exposed to different temperature during development. We call the performance curve the functions relating the average phenotypic expression of a fitness-related trait for sexuals and asexuals to a range of values of an environmental variable. .

Small to medium positive *d* values for other performance curves, quantifying nutrient contents (protein, lipid, sugar and glycogen: points 30, 31, 32 and 45), longevity (point 22), a measure of total fecundity in another study (point 54), fecundity at emergence (point 43) and developmental rate (point 36) according to temperature, indicate a higher plasticity in sexual forms. A measure for longevity yielded a negative value (point 21) but in this case, *d* did not differ significantly from 0. In contrast with these results are those for the performance curves for hind tibia length. For this measure, different results were obtained in two studies: either the two forms express similar curves (point 18) or asexuals show a larger breadth of the curve, suggesting higher plasticity (point 17). This difference in performance curves for size was mainly due to differential response at low temperature: lower decrease in size for asexuals when temperature decreases (a similar trend is observed for developmental rate by Foray et al., 2014 table 2). Interpreting the adaptive significance of the higher plasticity in size of asexuals is difficult because the relationship between size and fitness varies among insect species (Kazmer & Luck 1995; West et al., 1996; Ellers et al., 1998) and is unknown in *V. canescens*.

Overall, the results for performance curves are consistent with the hypothesis that individuals thriving in natural conditions have higher plasticity in responses to temperature than asexuals.

Response to intraspecific competition:

The tendency to superparasitize was measured by observing the behavior of females released in host patches previously exploited by sexual or asexual females. Point 7 shows that hosts parasitized by asexual females were more often rejected by other females (independently of their forms) than hosts previously parasitized by sexual females. There was no effect of the reproductive mode of second females on the incidence of superparasitism. Barke et al., (2005), in contrast, found that asexual females had a higher incidence of self-superparasitism. This could be adaptive under circumstance where the probability of conspecific superparasitism is high (Visser et al., 1990). However, their statistical analysis does not seem appropriate to handle random effects (female in this case) adequately.

Recognizing parasitized hosts allows females to assess the level of exploitation of a patch. When exploiting partly depleted host patches (i.e. in which some hosts are already parasitized), only asexual females decrease patch time (point 16). Sexual females experience low host encounters in nature and, hence should use very low marginal values and stay longer in partly exploited patches.

Discussion

The overarching hypothesis under test is that because sexual and asexual forms predominate in different ecological scenarios, anatomical and physiological traits will reflect adaptations to the circumstances of each form. Asexuals proliferate in stores, where hosts are clumped and there is no food for adults, while sexual breeders' hosts tend to be solitary (one per patch), spatially separated, and live in places where food for adult wasps is available. These distinct habitats made us predict that sexuals should show higher investment in flight capacity, longevity, and ability to

tolerate thermal changes, while asexuals will aim at the potential maximum reproductive output conferred by a larger egg-load which they, but not the sexuals, have opportunities to deploy.

Trade-off between current and future reproduction

Figure 1 displays the outcome of a large number of comparisons, many of which confirm our overarching hypothesis. Together, these results are clearly consistent with asexuals investing more in fecundity and sexuals more in locomotion and longevity. In environments with a higher rate of host encounter, a higher investment of asexuals in egg load is advantageous. Likewise, the asexual mode of reproduction provides an advantage over sexual lineages by the avoidance of the two-fold cost of sex caused by laying haploid eggs destined to produce males. On the other hand, the higher investment in locomotion and longevity in sexuals matches the host distribution and availability in the field. Facing scarce and spatially scattered hosts, the sexuals may be more often time-limited and die before having laid their whole egg-load. This would select for increased longevity. The effects of time limitation (dying before laying full egg supply) and egg limitation (defined as the temporary or permanent exhaustion of the supply of mature eggs), and how they mediate the trade-off between current and future reproduction, have been explored in various parasitoid species, and are an important aspect of the ecology and evolution of host-parasitoid systems (Rosenheim, 1996; Heimpel et al., 1998; Sevenster et al., 2000; Rosenheim et al., 2008).

Phenotypic plasticity in response to temperature

Wasps living in natural habitats have more general (breadth) performance curves and are less sensitive to temperature than those living in stores that are specialized to a narrow range of thermal values. Sexual wasps are less affected by temperature in their energy allocation to different functions (e.g. glycogen fuels flight function, Amat et al., 2012) ; this difference in plasticity may contribute to the difference in the resolution of the trade-off between egg production and

survival/locomotion in the two forms of *V. canescens*. In addition to being more plastic, sexual individuals are better able to tolerate extreme temperatures. Only sexual females, which live in variable weather conditions, adjusted their oviposition behavior when experiencing a sudden change in temperature (Amat et al., 2006). In line with these results, in sexuals, but not in asexuals, there is an accumulation of metabolites with a suspected cryoprotective functions in response to lower temperatures (Foray et al., 2013a; table 2).

Superparasitism

Hosts parasitized by sexual females are less likely to be rejected by later arrivals of either kind than those parasitized by asexuals. Why this is so needs further research. A possible causal explanation is that there are differences between the marking substances of the two forms, in either composition or quantity, which elicit different responses of later arriving females. A possible functional explanation would be that oviposition into a host already parasitized by a sexual wasps has a higher probability of resulting in an offspring, than oviposition into a host previously parasitized by an asexual female (van Alphen & Visser, 1990; Visser et al., 1992; Sirot 1996). While deserving further attention, results of Amat (2004) suggested such an asymmetry in competitive abilities of sexuals and asexuals in superparasitized larvae (for short time intervals between successive ovipositions).

Additionally, some studies considered the differences in cognitive abilities between sexuals and asexuals (learning color or odor cues related to resource availability, and time to take a decision in choice experiments) (Thiel et al., 2006; Lucchetta et al., 2007; 2008; Liu et al., 2009a and Thiel et al., 2013 in Table 2 Appendix A). Thriving in a more complex environment, sexuals are expected to benefit more than asexuals from being efficient at locating hosts and at learning local conditions (Stephens, 1993). In most cases the results were presented in terms of statistics

not suitable to be expressed into *d* values or reproductive mode is involved in higher-level interactions that impede to interpret its additive effect, thus these results cannot be incorporated to figure 1 and compared to other results.

Conclusions

Our comparison of life history traits between the two modes of reproduction in *V. canescens* shows that sexual and asexual individuals are each better adapted to the ecological niches which they occupy in a whole suit of characters. This conclusion is strengthened by the consistency between multiple observed differences, which are in accordance with the inferred selective pressures in both habitats. The life history traits that show the strongest relative divergences (high absolute values of *d* in Fig. 2) are those involved in the trade-off between egg load and adult survival or locomotion, and in the phenotypic plasticity in response to temperature. The consistency of the effect sizes obtained with individuals of both reproductive forms originating from different localities is a sound indication of their generality.

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576

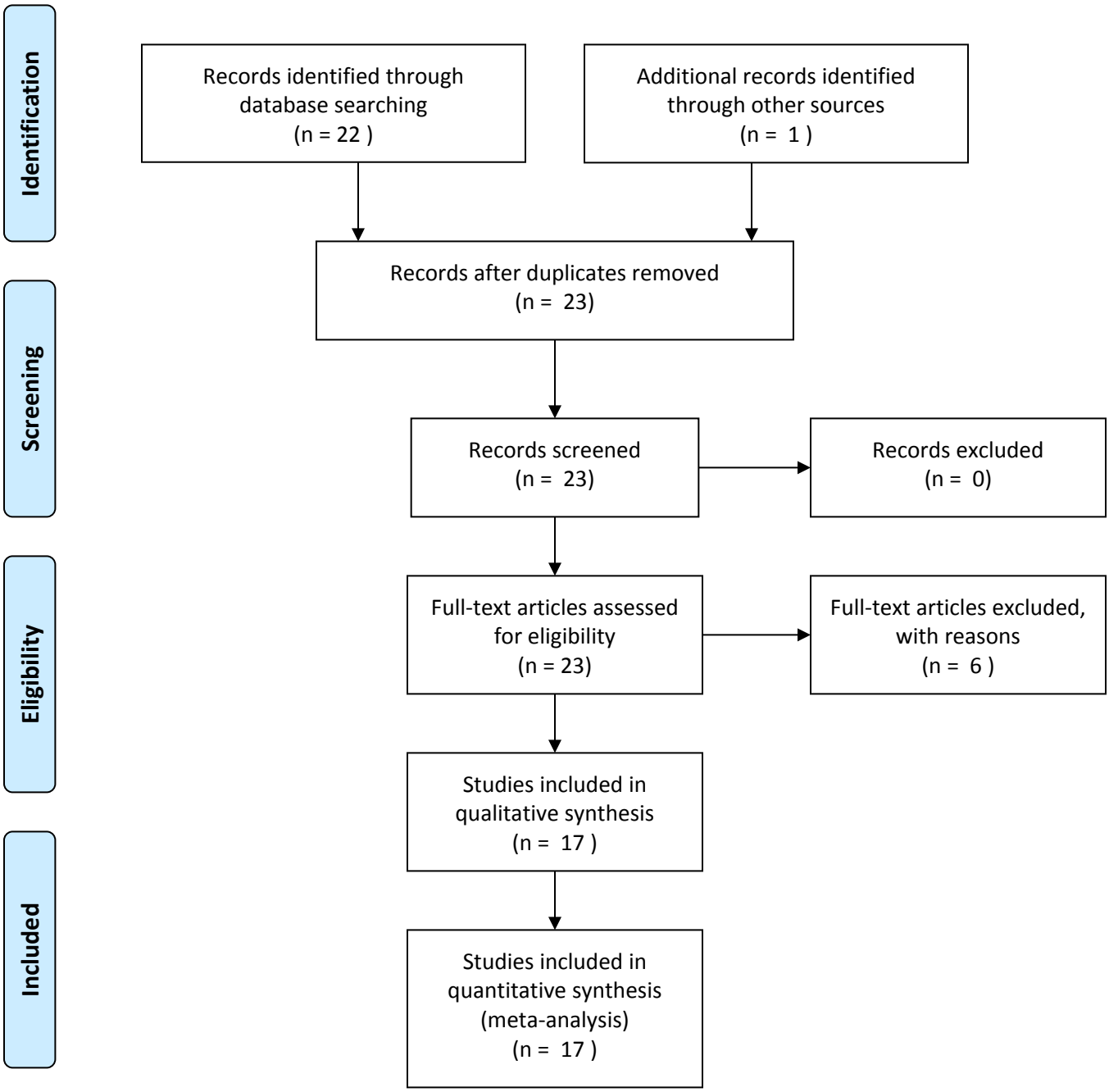
Legend

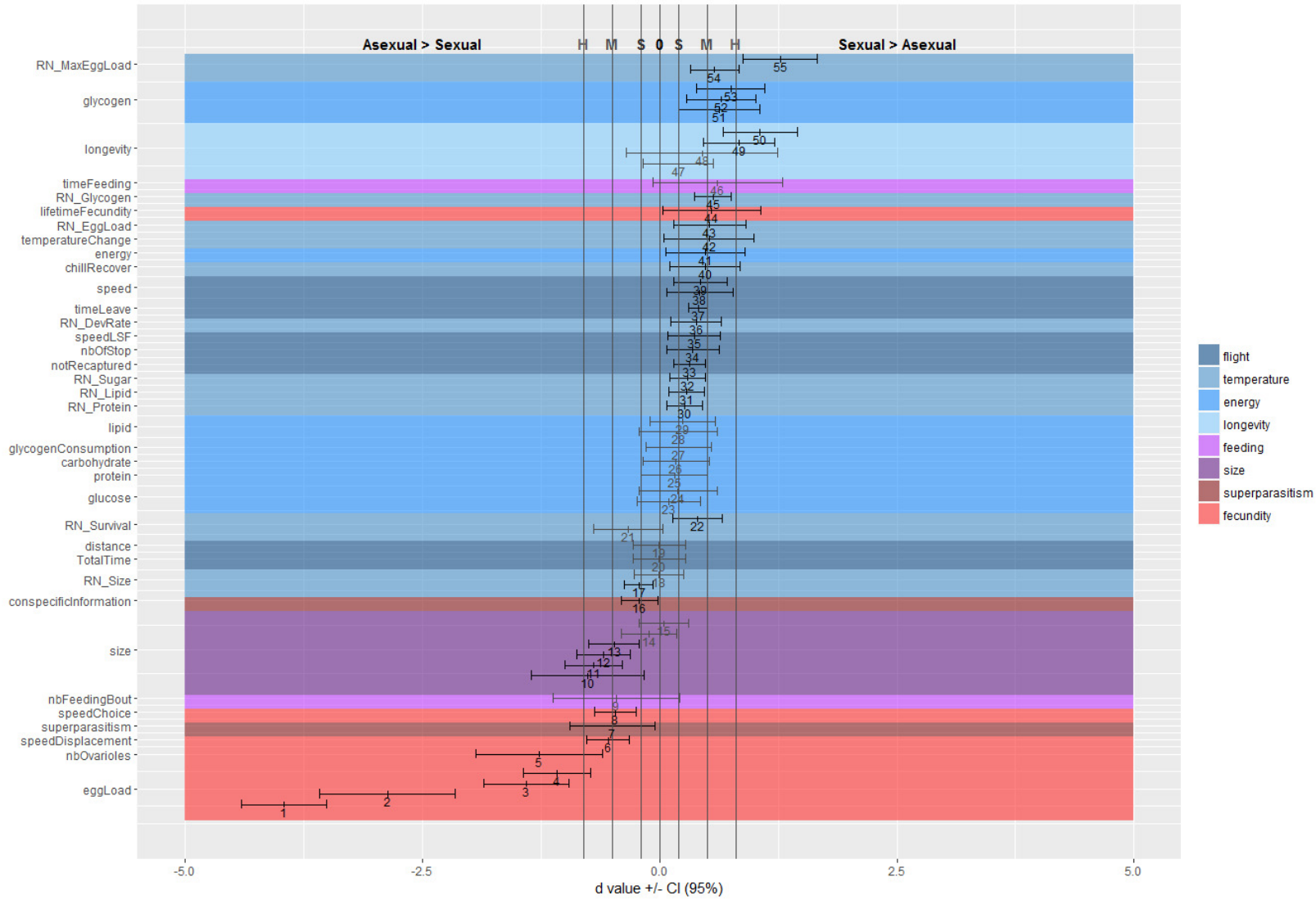
Figure 1. PRISMA flow Diagram describing the process of literature selection (from Moher et al. 2009)

Figure 2.

Standardized coefficients (Cohen's *d*) +/- 95% confidence intervals for the difference between asexual and sexual *V. canescens*. For ease of reading, the traits under study were pooled in 8 categories (size, fecundity, longevity, energy reserve, flight ability, feeding behavior, superparasitism and capability to deal with temperature changes). Positive *d* values indicate higher investment in the category under consideration for sexual animals. When dealing with reaction norms (RN, points 17-18, 21-22, 30-32, 36, 43, 45 and 54-55), positive *d* values stand for higher plasticity in sexuals (more breadth performance curve). Blue shades stand for categories where sexuals are expected to invest more than asexuals: longevity, energy, flight and capability to deal with temperature changes. Red shades stand for categories where asexuals are expected to invest: fecundity and use of conspecific information in the context of superparasitism. Purple shades are used for size and feeding behavior for which no clear expectations can be forecasted. The black line at *d*=0 indicates lack of statistical significance, and the grey lines at *d*=0.2 (-0.2), 0.5 (-0.5) and 0.8 (-0.8) indicate values over (below) which the difference is deemed “small” (S), "medium" (M) and “high” (H) (Nakagawa & Cuthill, 2007). Measures whose confidence intervals overlap 0 were figured in grey. See table 1 for each point signification and authority. speedLSF: speed of the longest single flight. Points are figured by ascending order of mean of the traits.

599 Figure 1


Identification
Screening
Eligibility
Included
Records identified through database searching (n = 22)
Additional records identified through other sources (n = 1)
Records after duplicates removed (n = 23)
Records screened (n = 23)
Records excluded (n = 0)
Full-text articles assessed for eligibility (n = 23)
Full-text articles excluded, with reasons (n = 6)
Studies included in qualitative synthesis (n = 17)
Studies included in quantitative synthesis (meta-analysis) (n = 17)


Asexual > Sexual
H M S 0 S M H
Sexual > Asexual
RN_MaxEggLoad
glycogen
longevity
timeFeeding
RN_Glycogen
lifetimeFecundity
RN_EggLoad
temperatureChange
energy
chillRecover
speed
timeLeave
RN_DevRate
speedLSF
nbOfStop
notRecaptured
RN_Sugar
RN_Lipid
RN_Protein
lipid
glycogenConsumption
carbohydrate
protein
glucose
RN_Survival
distance
TotalTime
RN_Size
conspecificInformation
size
nbFeedingBout
speedChoice
superparasitism
speedDisplacement
nbOvarioles
eggLoad
-5.0
-2.5
0.0
2.5
5.0
d value +/- CI (95%)
flight
temperature
energy
longevity
feeding
size
superparasitism
fecundity

600

Table 1

Authority, main results of the comparison between sexual and asexual strains included in Figure 1 and figures in the original article showing specific results. Category represents the 8 categories of measures we defined: size, 3 life history traits (Fecundity, Longevity, Energy level), 3 behaviors (Flight, Superparasitism and Feeding) and 1 plastic response to temperature change (Temperature); these categories referred also to those used in Figure 1. Data were obtained using strains collected at two different locations in France: in the vicinity of Antibes (Ant, 43°42'12.26" N - 7°16'50.33" E), and Valence (Val, 44°58′34″N - 4°55′6″E) and yearly renewed with freshly caught individuals.

Authors	**Results comparing sexual versus asexual *V. canescens ;* (origin of the strains)**	**Figures in original paper**	**Number in Fig. 2**	**Category**
Amat et al., (2012)	Egg-load at emergence; (Val)	1c	1	Fecundity
Barke et al., (2005)	Egg-load at emergence; (Ant)	7.4	2	Fecundity
Pelosse et al., (2007)	Egg-load at emergence; (Val)		3	Fecundity
Pelosse et al., (2010)	Egg-load at emergence; (Val)	1	4	Fecundity
Barke et al., (2005)	Number of ovarioles; (Ant)	7.5	5	Fecundity
Liu et al., (2009b)	Time to respond host odor; (Val, Ant)	1, 2	6	Fecundity
Amat et al., (2009)	Host propensity to be avoided for superparasitism; (Ant)	1	7	Superparasitism

Liu et al., (2009b)	Time to choose host patches differing in their quality; (Val, Ant)	1, 2	8	Fecundity
Pelosse et al., (2010)	Number feeding bouts; (Val)		9	Feeding
Pelosse et al., (2010)	Hind tibia length; (Val)		10	Size
Amat (2004)	Hind-tibia length; (Ant)		11	Size
Lukas et al., (2010)	Hind tibia length; (Val)		12	Size
Amat et al., (2012)	Hind-tibia length; (Val)	1a,b	13	Size
Pelosse et al., (2007)	Hind tibia length; (Val)		14	Size
Foray et al., (2011)	Hind tibia length; (Val)	1a	15	Size
Amat et al., (2009)	PRT in response to ovipositions in parasitized hosts; (Ant)		16	Superparasitism
Foray et al., (2014)	Reaction norm for hind tibia length at different temperatures; (Val)	2a	17	Temperature
Foray et al., (2011)	Reaction norm for hind tibia length as a function of temperature; (Val)	1a	18	Temperature
Lukas et al., (2010)	Total distance flown and total time in flight; (Val)		19, 20	Flight

Foray et al., (2011)	Reaction norm for longevity as a function of temperature; (Val)	2	21	Temperature
Foray et al., (2014)	Reaction norm for longevity at different temperatures; (Val)	3c	22	Temperature
Pelosse et al., (2010)	Glucose content; (Val)	2a, b	23	Energy level
Pelosse et al., (2007)	Glucose content; (Val)	1b, c	24	Energy level
Amat et al., (2012)	Protein content and free carbohydrates content; (Val)		25, 26	Energy level
Amat et al., (2012)	Glycogen consumption rates during flight; (Val)	2	27	Energy level
Pelosse et al., (2007)	Lipid content; (Val)	1b, c	28	Energy level
Amat et al., (2012)	Lipid content; (Val)		29	Energy level
Foray et al., (2014)	Reaction norm for protein, lipid and sugar content at different temperatures; (Val)	5	30, 31, 32	Temperature
Amat (2004)	Proportion of females not recaptured after release in flied conditions; (Ant)	28	33	Flight
Lukas et al., (2010)	Number of stops per flight of similar distance; (Val)	1	34	Flight
Lukas et al., (2010)	Speed of the longest flight; (Val)		35	Flight

Foray et al., (2011)	Reaction norm for development rate as a function of temperature; (Val)	1b	36	Temperature
Amat (2004)	Time to leave after experimental release; (Ant)	27	37	Flight
Amat et al., (2012)	Speed of flight; (Val)	3	38	Flight
Lukas et al., (2010)	Speed of flight; (Val)	2	39	Flight
Foray et al (2013b)	Time to recover from chill coma; (Val)	1	40	Temperature
Pelosse et al., (2007)	Teneral energy content; (Val)	1a	41	Energy level
Amat et al., (2006)	Change in the number of ovipositions in response to change in temperature ; (Ant)	3	42	Temperature
Foray et al., (2011)	Reaction norm for egg load at emergence as a function of temperature; (Val)	3a	43	Temperature
Barke et al., (2005)	Life-time offspring produced; (Ant)	7.2	44	Fecundity
Foray et al., (2014)	Reaction norm for glycogen content at different temperatures; (Val)	5	45	Temperature
Pelosse et al., (2010)	Time feeding; (Val)		46	Feeding
Barke et al., (2005)	Longevity of fed wasps at 29°C; (Ant)	7.6b	47	Longevity
Pelosse et al., (2010)	Longevity; (Val)		48	Longevity

Barke et al., (2005)	Longevity of fed wasps at 25°C; (Ant)	7.6b	49	Longevity
Foray et al., (2011)	Longevity; (Val)	2	50	Longevity
Pelosse et al., (2007)	Teneral glycogen content; (Val)	1d	51	Energy level
Pelosse et al., (2010)	Teneral glycogen content; (Val)	2c	52	Energy level
Amat et al., (2012)	Glycogen content; (Val)	2	53	Energy level
Foray et al., (2014)	Reaction norm for maximal fecundity at different temperatures; (Val)	3b	54	Temperature
Foray et al., (2011)	Reaction norm of maximal egg-load as a function of temperature; (Val)	3b	55	Temperature

609

610 **Appendix A**: literature selection and *d* calculation

611 *Selected literature for the meta-analysis*: We calculated the effect size of
612 reproductive mode for the great majority of the 46 traits under study from the 16 papers
613 included in the meta-analysis (see also "overview of the selected literature" section in the
614 main text). Some results, indicated in Table 2, were not included in Figure 1 because either
615 a) higher-level interactions impede to interpret the additive effects of reproductive mode
616 and thus to calculate *d* statistics for these effects (note that when reproductive mode is
617 involved in higher-level interactions but without switch of effect in each reproductive
618 mode, additive effects of mode of reproduction are provided, e.g. point 34 in Fig. 2); b)
619 experimental design did not compare the sexual and asexual trait in a single experiment; c)
620 *d* inappropriate for the statistics used (*e.g.* non or semi- parametric statistics, multivariate
621 analysis) ; d) the information provided did not allow for statistical comparisons in terms of
622 *d* values.

623

624 **Table 2**

625 Authority and main results of the comparison between sexual (S) and asexual (A) strains that are
626 not included in Figure 1. Figures in the original paper showing specific results. Comment: reasons
627 that led to their exclusion from Figure 1 (see text for details). PRT: patch residence time. Origin
628 of the strains: Ant, Antibes (France), and Val, Valence (France). In two cases some results were
629 considered redundant. In Amat et al., (2006) two similar experiments gave similar results. In Lukas
630 et al., (2010) in the same experiment similar measures of flight performance yielded similar results.
631 In these two cases a single result was included in Figure 1.

Authors	Results of comparing sexual versus asexual *V. canescens ;* (origin of the strains)	Figures in original paper	Comment
Amat (2004)	Recapture rate in the field: 11% of all captures in field transects are A and 89% S. In 19.5 % of the samplings A and S coincided in recapture date and location (Val)	22, 24	*d* inappropriate
Barke et al., (2005)	Higher Longevity for fed S at 15 °C (Ant)	7.6	*d* inappropriate
	No significant differences in longevity for unfed A and S at 15,25 and 29 °C (Ant)	7.6	*d* inappropriate
Liu et al., (2009a)	PRT depends on "travel time" : S use flying time between two successive patch encounters while A simply use waiting time (either flying or resting) (Ant, Val)	4	Experimental design
Lucchetta et al., (2007)	The effect of the number of ovipositions on PRT is differently affected by the mode of reproduction (A or S), depending on the origin of the animals (Ant or Val). For the wasps from Antibes, each oviposition decreases stronger the PRT in A than in S. In Valence, the effect of the number of ovipositions is independent of the reproductive mode (Ant, Val)	4	Higher level interaction
Lucchetta et al., (2008)	No difference between A and S in their ability to learn a color associated with a food reward (Val)	3	*d* inappropriate
Foray et al., (2014)	The shape of the performance curve for developmental rate differs with the reproductive mode: S females reach higher maximal growth rate than the A females do. The shape is also affected by the thermal regime, with a decrease of the developmental growth rate at 25 and 30 °C under the fluctuating regime (Val)	2b	Higher level interaction
Foray et al., (2013a)	Metabolite profile differences in response to thermal change: phenylalanine, threonine and serine were more abundant in the S, while maltose, succinate, sucrose and glycerol were more abundant in the A (Val)	2	*d* inappropriate

Pelosse et al., (2007)	The relationship between egg load at death and longevity: resource availability during ontogeny and reproductive mode affect this relationship. When resource are highly available, S live longer than A and have fewer eggs than their A counterparts. When the A and S wasps develop in low resource available conditions, they decrease both in fecundity and longevity (Val)	2	Higher level interaction
Pelosse et al., (2010)	Fructose amounts during lifetime is affected by size in interaction with reproductive mode (Val)	2a, b	Higher level interaction
Thiel et al., (2006)	No differences in giving up time between S and A (Ant, Val)	3	Insufficient information and higher level interaction
	A reduce their PRT with successive visits to patches in a rich environment (in terms of host patches); in contrast, S females do not modify their behavior with experience (Ant, Val)	4	Insufficient information and higher level interaction
	Higher oviposition rate with successive visits to host patches in A than in S (France: Ant, Val, Nice, Valbonne, Golf-Juan; Italia :Tuscany; Portugal: Algarve)	8	Insufficient information
Thiel et al., (2013)	S are not more effective learners than A females in a context of associative learning of stimuli related to hosts (Ant, Val , Mont Boron)	3	*d* inappropriate Low sample size

632

633 *Statistical analysis:* When reared on its host *Ephestia kuehniella*, asexual *V. canescens* tend to be
634 larger than their sexual counterparts (differences in hind tibia length indicated by points 10-15 in
635 Fig. 2. See points 14 and 15, for non-significant differences). In most of the original analysis
636 performed in papers listed in table 1, trait measurements are corrected for size by taking the size
637 as the first covariate in statistical models. This allows revealing the differential investment effort
638 in traits for individuals of the two modes of reproduction.

639 To integrate and interpret the results of a large set of publications dealing with the
640 differences between sexual and asexual *V. canescens*, we standardized the mean differences
641 between strains in terms of the standard deviations of the difference. This yields effect size
642 measurements (Cohen's *d* value, Cohen, 1988) devoid of units and thus comparable in a meta-
643 analysis approach. *d* is defined as

644 $$d = \frac{m_1 - m_2}{S_{pooled}}$$

645 with

646 $$S_{pooled} = \sqrt{\frac{(n_2 - 1)s_2^2 + (n_1 - 1)s_1^2}{n_1 + n_2 - 2}}$$

647 where m_1 and m_2 are the mean values for two groups, s_1^2 and s_2^2 are the variances and n_1 and n_2
648 are the sample sizes.

649 The parameter *d* might be calculated using different expressions. We used the expression suggested
650 by Nakagawa and Cuthill (2007)

651 $$d = \frac{t(n_1 + n_2)}{\sqrt{n_1 n_2 df}}$$

652

653 where *t* is Student's statistic obtained from the statistical analysis and *df* is the number of degrees
654 of freedom used for a corresponding *t* value.

655 The approximated 95% confidence intervals (95% CI) of *d* are given by

656 *95% CI= d-1.96 × se_d* to *d+1.96 × se_d*

657 where se_d stands for the asymptotic standard error. There are several mathematical expressions
658 that allow for the calculation of this value. Here we used (Hunter and Schmidt 2004)

659 $$se_d = \sqrt{\left(\frac{n_1 + n_2 - 1}{n_1 + n_2 - 3}\right)\left[\left(\frac{4}{n_1 + n_2}\right)\left(1 + \frac{d^2}{8}\right)\right]}$$

660 This expression is adequate for Cohen's *d*, although it might provide biased estimates for small
661 sample sizes. We calculated both biased and unbiased estimates. The differences between biased
662 and unbiased estimates proved to be negligible (results not presented). The results of the analysis
663 of continuous response variables performed by means of generalized linear models express the
664 significance of a given process in terms of *F* values. As two groups were compared, the number of
665 degrees of freedom for the treatments is 1, and *t* can be calculated as suggested by Nakagawa and
666 Cuthill (2007):

667 $$t_{n\,\mathrm{df}} = \sqrt{F_{1,n\,\mathrm{df}}}$$

668 When statistical models expressed significance in terms of the normal distribution, in the relevant
669 equations we used the *z* values to replace the *t* values, calculating the degrees of freedom as if *t*-
670 tests were used (Nakagawa and Cuthill 2007).
671
672 In these calculations, positive *d* values stand for the case where a trait value is higher in sexuals.
673 In some cases, the trait measured is negatively correlated with the investment in the category under
674 study. These cases are: number of stops during a flight covering a given distance (negatively
675 correlated to flight investment because this implies shorter flight bouts, point 34 in Fig.1); time to

676 leave release apparatus in the wild (negatively correlated to flight investment, point 37 in Fig.1)
677 and time to recover from chill coma (negatively correlated to ability to deal with changing
678 temperature, point 40 in Fig.1). In these cases, we changed the sign of the *d* value. In this way, in
679 Figure 1 all positive *d* values correspond to cases where sexuals invest more than asexuals in a
680 given trait (size, fecundity, longevity, energy level, flight, superparasitism, feeding and
681 temperature). When dealing with reaction norms (points 17-18, 21-22, 30-32, 36, 43, 45 and 54-
682 55 in Fig. 2), positive *d* values stand for higher plasticity in sexuals. This corresponds to situations
683 in which i) sexual parasitoids present shallower and broader curves, allowing high reproduction
684 rates for a wider range of temperatures, and ii) asexual wasps, having narrower response curves,
685 maximize reproductive success under a restricted thermal range.