Genetic variation of traits in natural enemies relevant for biological control: a systematic review

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Abstract

The concept of genetic improvement in relation to biological control involves the exploitation of natural genetic variation for the benefit of existing biological control agents (BCAs). Despite recent calls for this process to be adopted in biological control research, there is no clear overview of the current state of research into genetic variation within a biological control context, including quantifiable estimates such as narrow-sense heritability (h^2). In this systematic review, we aim to determine the current state of research on the genetic variation of biological control traits in natural enemies. After the searching process, screening for papers that can deliver on our research question reduced the initial 2,927 search hits to only a mere 69 papers for data extraction. Of these, the majority (73.6%) did not report quantitative values for genetic variation. Extracting the traits measured in these papers, we categorized them according to two approaches; the first related to fitness components, and the second related to biological control importance. This systematic review highlights the need for more rigorous reporting of the quantitative values of genetic variation to enable the successful genetic improvement of biological control agents.

Keywords

Genetic improvement, genetic variation, heritability, systematic review, biocontrol agent, life history traits

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1. Introduction

With a rising global population, as well as a changing global climate, food production is increasingly under pressure (IPCC, 2007; Misra, 2014). Rising arthropod pest pressure (due to modern monoculture practice as well as expanding pest ranges related to global change (Das et al., 2011)), coupled with a desire for more environmentally sustainable agriculture (i.e. using less pesticides) (Rigby and Cáceres, 2001), has led to an increased interest in biological control for pest management (van Lenteren et al., 2018). The use of arthropod natural enemies as biological control agents (BCAs) is not new, with records of first releases dating back over 100 years (Barratt et al., 2018). For several decades, imported exotic natural enemies were relied upon to control non-native pests, which are becoming increasingly more prevalent due to expanding or shifting ranges linked with changing climates (Aguilar-Fenollosa and Jacas, 2014; van Lenteren et al., 2006). By taking the natural enemy from the native range of the pest, it was considered to be better adapted to tackling the pest due to their shared evolutionary past. Due to knowledge gained on the risks of releasing non-native species, along with stricter regulations on the import and export of species (such as the Nagoya Protocol on Access and Benefit Sharing, 2010), this practice has become less desirable (CBD Secretariat, 2011; Lommen et al., 2017). These recent developments in combination with an expansion of pest ranges due to global warming and the anthropogenic movement of produce across the globe, make it more important than ever to improve the efficacy of those native natural enemies that are already at our disposal (Leung et al., 2019; Lommen et al., 2017).

Selection of effective BCAs is usually determined at species level, by looking at interspecific variation (Lommen et al., 2017), i.e. finding the best species to tackle a certain pest. More recently, there is increased attention on exploiting the large amount of intraspecific variation between, and even within, populations (Kruitwagen et al., 2018; Lommen et al., 2017). Recent studies have also suggested the use of genetic modification for increased effectiveness of BCAs, particularly in fungal and pathogen-based agents (Karabörklü et al., 2018; Lovett and St. Leger, 2018; St. Leger and Wang, 2010), as well as insects (Poppy and Powell, 2009; Routray et al., 2016). However, as with using genetically modified crop plants, the release of genetically modified natural enemies would come under strict regulation (Barratt et al., 2018; Reeves et al., 2012) and does not seem compatible with the eco-friendly mission of biological control. On the other hand, artificial selection of traits is an accepted method already commonly used across agriculture, such as in livestock and plant breeding (Brotherstone and Goddard, 2005), which can be exploited to effectively improve BCAs (Kruitwagen et al., 2018; Lommen et al., 2017).

A recent review on the use of experimental evolution in biological control supports the potential of artificial selection for improving BCAs (Lirakis and Magalhães, 2019). The key prerequisite for artificial selection is the presence of genetic variation for the trait of interest. The prime estimate of genetic variation is heritability, which is defined as the proportion of the total variation between individuals in a defined population that is due to genetic variation (Lommen et al., 2017). Heritability or evolvability is regularly studied within the realm of basic and evolutionary research, and often so with insects due to the ease of their rearing and workability in a controlled laboratory setting. However, it has been studied to a lesser extent within an applied context. This can be to the detriment of BCAs and their effective use, both in regards to deleterious impacts of genetic drift and subsequent loss of efficacy (Paspati et al., 2019; Szűcs et al., 2019), and that without variation data for traits of interest, there is no way of knowing if the trait in question can be improved through genetic selection (Houle, 1992). As for the latter, full reporting or values such as variance and determining evolvability in place of heritability values was proposed more than twenty years ago (Hansen et al., 2011; Houle, 1992) as a more appropriate measure, yet the uptake has been slow and inaccurate calculations remain a concern (Garcia-Gonzalez et al., 2012).

With the increased interest in the role of experimental evolution and artificial selection in the improvement of biological control (Kruitwagen et al., 2018; Leung et al., 2019; Lirakis and Magalhães, 2019; Lommen et al., 2017; Routray et al., 2016), it is necessary to determine what has already been assessed with regards to genetic variation and heritable traits of BCAs, and where there are gaps in our knowledge.

In this systematic review, our goal is to compile and summarize findings from across literature regarding genetic variation in BCAs for traits that are potentially useful for biological control, regardless of whether these studies have an applied focus or not. This will identify the advances already made with regards to identifying suitable heritable traits within arthropod BCAs, and where more work is necessary.

2. Methods

2.1 Search Criteria

As the steps of a meta-analysis and systematic review are similar up until the data extraction phase (Côté and Jennions, 2013) for searching, screening, and the extraction protocol, we followed the steps outlined in Chapter 2 of the Handbook of Meta-Analysis in Ecology and Evolution (Koricheva et al., 2013). An overview of the process is provided in Figure 1. Our question was refined to a single search term that focused on two aspects: BCAs and genetic variation or heritability. We did not wish to limit our initial search results by *a priori* defining traits of interest.

The databases used were CAB Abstracts (1910 to 2019), the Biological Abstracts database (1969 to 2016), and the Agricola database (1970 to April 2019), which were all accessed via the CAB Abstracts search platform. Additional search parameters were chosen, including using the "field= keyword" search field (searching for terms in the title, abstract, or keywords), as well as limiting document type to 'Article' and 'Review.' No language restrictions were imposed at the time of the search.

To validate our search term, a positive control group was set up of 15 papers that would suit the purpose of initial screening for our research question. This set of controls can be found in the Appendix (Table S1).

As we were interested in finding publications that assessed genetic variation or heritability of different traits of BCAs, the search term contained various terms and wildcard symbols `(*)` to aid in the search, as well as the `AND/OR` operator to tie the two ideas together. To limit the search to arthropod BCAs, the `NOT` operator was used in conjunction to avoid the inclusion of several undesired returns.

Consequently, the final search term was as follows:

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("genetic varia*" OR "genotypic varia*" OR heritab*)

AND (enem* OR predat* OR parasitoid* OR "parasitic wasp*" OR
biological control OR biocontrol)

NOT (virus* OR nematode* OR weed* OR fung*)
```

Initial search hits were deduplicated using the duplication removal tool found within the CAB Abstracts search tool (based on *Abstract*). The total bibliographic information for these hits were downloaded and arranged into a table for further screening. Search queries were performed on September 17, 2018 and May 16, 2019.

Duplicate entries overlapping both search periods were removed manually, while some duplicates remained in the dataset until screening. Importantly, all positive controls were returned in the search results.

2.2 Screening search results

Unique entries were subject to a preliminary screening that sought to determine, based on title, abstract, and any keywords whether the entries were appropriate for the systematic review. This initial screening was performed by a team of 16 readers, and was based solely on content related to study species: first, if the species of study (as determined in the title or abstract) was truly an arthropod; and second, if the species of study was classified as a BCA by checking whether it appeared on either the EPPO list of BCAs available for use in Europe (PM 6/003, both 2016 and 2019 versions, https://gd.eppo.int/standards/PM6/), or on the list of BCA species compiled in previous reviews (van Lenteren, 2012; van Lenteren et al., 2018). This list contains 361 species names, some of which are former scientific names that are no longer in use, but allow for scanning older papers.

Two additional screening measures occurred: on language and availability. First, language was either listed as a variable from the database bibliographical information or was assessed by viewing the full text of the entry. Languages that were understood by our team of readers were assessed, while languages not understood by the team remained unassessed. Second, unavailable entries were listed as 'missing', that is, while the entry existed in one of the three databases used for the initial search, neither electronic nor physical records in the Wageningen University Library network were available and additional online queries yielded no records.

Remaining duplicates (based on entry title), as well as conference proceedings, were removed manually.

At this point, each entry in the dataset corresponds to a single peer-reviewed article. The final screening category was 'relevance'. Relevance to the review terms was evaluated based on the article's abstract, title, or full-text in some cases, and was determined based on two parameters: 'methods' and 'trait of interest'. If the methods allowed for determining of genetic variation, the article was deemed relevant. Such methods would include the use of isofemale lines, tracking over multiple generations, common garden set-ups, parent-offspring regressions, or a type of sibling or crossing strategy. For the second parameter, 'traits of interest', it was the presence of any kind of phenotypic trait being studied that was important. For instance, articles that solely focused on population structure via neutral molecular markers, but were not looking at phenotypic traits, were deemed unrelated to this systematic review. All articles determined to be relevant were then subjected to full-text assessment and data extraction.

2.3 Data extraction and categorization

In-depth data extraction was performed by six readers, with a follow-up by two readers to double-check the values of the extractions. Each article was viewed in print and assessed for the following aspects: 1) estimation method, 2) trait of interest, 3) species, and 4) population values (such as size and number of populations). When applicable, a wide range of variables related to each trait and population that were assessed in the study were extracted as well. Interest was paid to values directly informative of genetic variation, such as narrow-sense heritability (h^2), broad-sense heritability (H^2), or evolvability (CV_A) estimates. For a single article, several unique data extraction outputs (termed 'observations') are possible, and all received a unique identification number in order to track the total data extracted. This granularity allows for assessing how often a trait is measured for different populations or species in various studies, as multiple unique values related to genetic variation of traits of interest are possible for a single article.

For each trait of interest, categories were assigned to each observation to refine the extraction data to clear themes. Two categorical systems were used. The first system uses the categories of phenotypic traits based on biological function as defined by Mousseau and Roff (1987): physiology (P), morphology (M), life history (L), and behavior (B) (Mousseau and Roff, 1987). These categories are explicit, and each trait can only be attributed to a single category. The second system is based on the application of biological control and uses categories as defined in Leung et al 2019, which posits four aspects of biological control that could be improved using genetic knowledge: pest suppression ability (1), adaptation to abiotic factors (2), reducing ecological risk (3), and improving mass rearing conditions (4). Three additional categories were created to address the outcomes of this extraction, and include: insecticide resistance (5), adaptation to biotic factors (6), and a null category named 'unrelated' (7), as to avoid forcing a trait into one of the other six categories. This second classification is not explicit, and one trait may be attributed to multiple categories. Simple calculations (counts and means) were performed manually, while figure generation was performed using R (version 3.5.0), R Studio (version 1.2.1335), and ggplot2 (version 3.2.0)(R Core Team, 2015; RStudio Team, 2015; Wickham, 2016).

3. Results

3.1 Search results

The first search using the full search term yielded 3,612 hits but was reduced to 2,880 following deduplication (Figure 1). The second search, carried out eight months later, yielded 3,471 hits, and deduplication reduced it to 2,891. This includes new articles published as well as any entries added to any of the three databases within the intervening period. From the second search, 87 unique hits were found that cover the period between the first and second searches (September 2018 to April 2019). Overlapping hits were removed by hand, resulting in a total of 2,927 hits for the systematic review. It is worth noting that some hits that were in the first search were no longer present in the database for the second search. The complete dataset of search returns at this point are available in the Appendix (Table S2) in the format delivered by the CAB Abstracts Database.

Results of this combined search return, according to year of publication, can be found in Figure 2. Year of publication ranges from 1914 to 2019. Several years in the earlier time of the search returned no hits, representing the true minimum. Fifteen different years are represented by only a single hit, while the maximum belongs to 2014 with 181 entries. Values skew closer to the present-day, likely attributed to both the well-documented increase in scientific publishing (Larsen and von Ins, 2010) and a general increase in biological control studies. Similar results occurred in a recent review on zoophytophagous predators (Puentes, Stephan, and Björkman, 2018). The majority of returns are from the CAB Abstracts database (1304), which was chosen as the preferred database for the search and deduplication, followed by Biological Abstracts (969), and Agricola (654).

3.2 Screening

Preliminary screening was performed to remove all the entries that were non-arthropods, not on the EPPO or van Lenteren lists, or those that were problematic (duplicates, missing, or languages unavailable to readers). From the 2,927 entries, only 1,606 were entries containing arthropod research (1,321 non-arthropods were removed). From these 1,606, only 393 were determined to be species that were on the combined EPPO and van Lenteren 2012 list of BCAs. All remaining duplicates were removed manually (94) along with conference proceedings (3), resulting in a total of 296 articles.

At this point, several articles were identified as problematic, either for availability or language. Four papers were identified as missing and were removed from the dataset. Eighteen articles were not in English. Most of these articles were in Chinese (9), followed by Portuguese (3), Russian (3), Czech (1), German (1), Persian (1), Spanish (1), and French (1). Where possible, articles were assessed by native speakers with a biological background to determine relevance, followed by non-native but fluent speakers with a biological background. All foreign language papers could be assessed with the exception of all three Portuguese papers and one Russian paper. These four unassessed papers were deemed unrelated, followed by an additional eight papers that were assessed. Of the 20 non-English papers, seven were assessed and kept for further screening. This final step reduced the articles in this dataset to 279, all of which are listed in the Appendix (Table S3).

3.3 Extraction

Of the 279 screened articles, only 69 were ultimately deemed relevant to this systematic review, based on the estimation methods and presence of measured traits, and are listed in Table 1. Results from the extraction process, with reduced variable extractions for each extraction output, can be found in Table 2. The amount of observations depends on the species studied, the number of populations assessed, and the trait of interest. For example, one paper may look at a single trait in two species using isofemale lines, which would result in two observations. Within our results, there are 302 observations in total: 137 for parasitoids, and 165 for predators. Per paper, the average number of observations is 4.4, however, a small number of papers exceed 10 observations, and can therefore account for any skewing of popularity in estimation methods or species interest. For example, the most observations per species belong to *Harmonia axyridis* with 50 observations, while only being found in five papers. While the full dataset is informative for traits of interest, other parameters such as year of publication or estimation method will be better observed by reducing to unique observations.

Focusing on publication year, the spread of articles that reach the extraction phase is relatively well-distributed from 1979 to 2018 with no clear bias towards the present day (Table 1). Moving on to the BCAs themselves, there are 29 different species studied in this dataset, 13 of which only appeared once (Table 2). The most studied species in our dataset is the parasitoid *Aphidius ervi*, which was covered in eight articles. The parasitoid *Trichogramma* is the most studied genus of the extraction with 12 articles, followed by *Aphidius,* with eight articles. Considering the genetic variation estimation methods (Figure 3), just over a quarter of observations used isofemale populations to estimate inheritance (27.1%), followed by artificial selection (17.1%).

Despite the use of these estimation methods, the majority of papers did not provide heritability estimates. We limited this to values of broad-sense heritability (H^2) and narrow-sense heritability (h^2), as well as evolvability (CV_A). In some cases, these estimates were not reported directly, but we were able to convert the reported genetic or dominance variance into these estimates using other data reported in the paper. Of our 302 observations, only 105 were supported by measures of genetic variation. When reduced to unique species per paper (72, as a few papers cover two species), 19 provided a heritability estimate for the trait assessed as opposed to the 53 (73.6%) that did not (Figure 4). The most commonly used were either h^2 (9.7%) or H^2 (8.3%), followed by either in combination with CV_A (h^2 and CV_A at 4.2%, and H^2 and CV_A at 2.8%), CV_A on its own (1.4%), or both broad and narrow sense heritability at the same time (1.4%). These amounts include papers where we were able to calculate estimates using reported data in the text. Papers that reported on variations of CV_A nearly always reported CV_G, but in the cases referenced here these were found to be referring to the same measure (CV_A). Meanwhile, the majority of papers did not report any heritability estimates or include values necessary for their calculation.

An important goal of our analysis is the categorization of traits according to fitness component, or importance to biological control research. Given the variety of traits being measured, both in nomenclature and formulation, categories were assigned and pooled by observation count in two ways: the Mousseau and Roff assessment based on biological function used in their review of the heritability of fitness components, and the Leung et al. 2019 assessment based on biological control application (Mousseau and Roff 1987; Leung et al. 2019). The outcome of the Mousseau and Roff assessment indicates that the majority of the 302 observations were of life history traits (53%), followed by behavior (21%), morphology (19%), and physiology (7%; Figure 5). Also within the different BCA types, parasitoid or predator, life history is still the most accounted for trait for both types, while behavior and morphology switch middling positions depending on BCA type.

The second assessment method, based on biological control application (Leung et al 2019), allowed for multiple classifications per observation (364 total). As shown in Figure 6, the majority of the traits measured were related to pest suppression ability (53%), followed by improving mass rearing conditions (23%). The third most common classification of the observations was the 'unrelated' category with 13% of the observations and the traits associated with them were most likely not useful for improving biological control directly.

4. Discussion

This systematic review sought to identify studies on BCAs that look at the genetic variation and heritability of traits and ordered these traits by two classification systems. According to the Mousseau and Roff classification, a majority of studies dealing with trait heritability focused on life history traits, regardless of BCA type. The other classifications of Mousseau and Roff (morphology, behavior, and physiology) were also approached in various heritability studies, but to a much lesser extent than those focusing on life history traits. This is most probably due to the importance of life history traits for biological control, which resulted in a large body of descriptive literature for BCAs (Mayhew, 2016). Furthermore, life history traits are generally considered to be an established measure of an organism's reproductive strategy and, ultimately, fitness. As such, they are considered important in the establishment and success of BCAs (Plouvier and Wajnberg, 2018). They are also wide ranging and can vary from obvious characteristics such as longevity and number of offspring, to more specific attributes such as conversion efficiency, certain of which are proven to be very useful in particular applied settings. Of the papers in the final selection, 30.6% were found to include usable heritability estimates or the means to calculate them.

The functionality of traits in a biological control setting was further explored using the second classification. This classification gives a more targeted approach to labelling traits as to their potential utility in a biological control setting. The majority of traits analyzed within this set were attributed to 'pest suppression ability'. This attribute would include traits classed as life history traits in the Mousseau and Roff classification (i.e. number of offspring or sex ratio), but could also include certain behavioral traits (i.e. patch residence time). In terms of number of observations, the next group of traits are those 'useful in improving mass rearing conditions', which would include life history traits such as sex ratio. These are potentially two of the more important classes within the classification for biological control application, indicating that the traits outlined in Leung et al. are in line with the current trends in biological control research (Leung et al., 2019). It is also important to note that certain traits could fit into several of the biological control trait classifications, whereas the Mousseau and Roff classifications are clear-cut. In this way, the classification for biological control application could be deemed more relevant or concise when narrowing down traits for their importance in biological control, and by doing so in such a study as ours, pinpoints those that are also heritable. Our results further show that traits related to 'adaptation to biotic factors,' and 'reducing ecological risk' are relatively understudied compared to the others, which could be seen as an incentive for more studies.

The lack of data on genetic variation in our results does not necessarily represent a lack of heritability studies - indeed in our original search we found 69 papers concerning heritability of life history traits in BCAs with appropriate estimation methods. Of these, however, only 19 papers contained heritability values, either in the form of broad-sense heritability, narrow-sense heritability, evolvability, or the genetic and environmental variance estimates required for calculation. As for estimation methods, nearly 9 out of 10 papers were removed from the analysis during our screening due to opaque reporting of methods and results, yet the papers still referenced heritability or genetic variation. This opacity has been documented previously, such as in a recent review on the use of experimental evolution to improve biological control, where the majority of studies found did not carry out replicates or maintain control populations (Lirakis and Magalhães, 2019). Discrepancies such as these are indications of the flexibility of terms and experimental design between research disciplines; the full reporting of values is simply a recommendation for improving research on genetic variation that has been made before (see Houle, 1992). Reporting sample size is necessary for variance calculations, whereas calculating heritability values is encouraged in order to add quantitative data to a discussion on heritability. With this in mind, it became clear during the extraction of data that further analysis, such as a meta-analysis of the heritability results, would be intractable. This is due to the wide spread of species and traits of interests juxtaposed to a lack of heritability values and other values necessary for such an analysis. This lack of reporting could be due to oversight or publication restrictions (such as limitation on manuscript length or perceived triviality of some data), but another possibility is that the perceived importance of reporting these values is not high. We hope that recent calls on the importance of genetic variation for improving BCAs, such as Leung *et al.* (2019), and the need for these values will shift towards studies publishing more basic information and additional data in the future.

Finally, there are fairly similar number of papers on parasitoids and predators, both before and after extraction. While initially there looked to be a slight bias towards parasitoids, there is a larger bias in the registered and published BCA types in use, with far more parasitoids than predators (van Lenteren, 2012), making this more-or-less equal outcome more surprising.

This systematic review was carried out across three different reference databases with an intentional search term that was tested against positive and negative controls. Once the search results returned, assessment of the study for its inclusion was based on both objective and subjective measures. In this respect, certain papers that would fit the desired outcome of the search may have been absent due to database or search term or dismissed prematurely due to human error. Taxonomic changes could also play a part in missing papers that would otherwise be suitable for this analysis. Finally, refining the species studied to the combined list of the 2016 and 2019 EPPO lists of commercial BCAs (PM 6/003) as well as using a commercial list from 2012 that was updated in 2018 (van Lenteren, 2012; van Lenteren et al., 2018) may remove any species that are currently being investigated as a potential BCA.

5. Conclusion

The results of this systematic review indicate a variety of research and interest in studying the heritability of traits in BCAs and can act as a starting point for improving natural enemies. The presence of genetic variation for traits related to biological control supports the calls for improvement of biological control agents via natural genetic variation made previously (Kruitwagen et al., 2018; Leung et al., 2019; Lirakis and Magalhães, 2019; Lommen et al., 2017). Indeed, a large variety of groundwork has been established in these fields related to species, estimation methods, and traits of interest. However, studies that report on genetic variation cannot necessarily add to the advancement of biological control research if heritability estimates and associated values are not reported. With this in mind, this aspect of biological control research is ripe with opportunities, and several of the studies we have profiled here are an excellent starting point for the genetic improvement of the efficacy of biological control agents.

CRediT Author Statement

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Declaration of interest

The authors declare there is no conflict of interest.

Appendix

Supplementary material indicated in this manuscript (Tables S1, S2, and S3) are available on the DANS EASY Repository, https://doi.org/10.17026/dans-zvv-d2dr.

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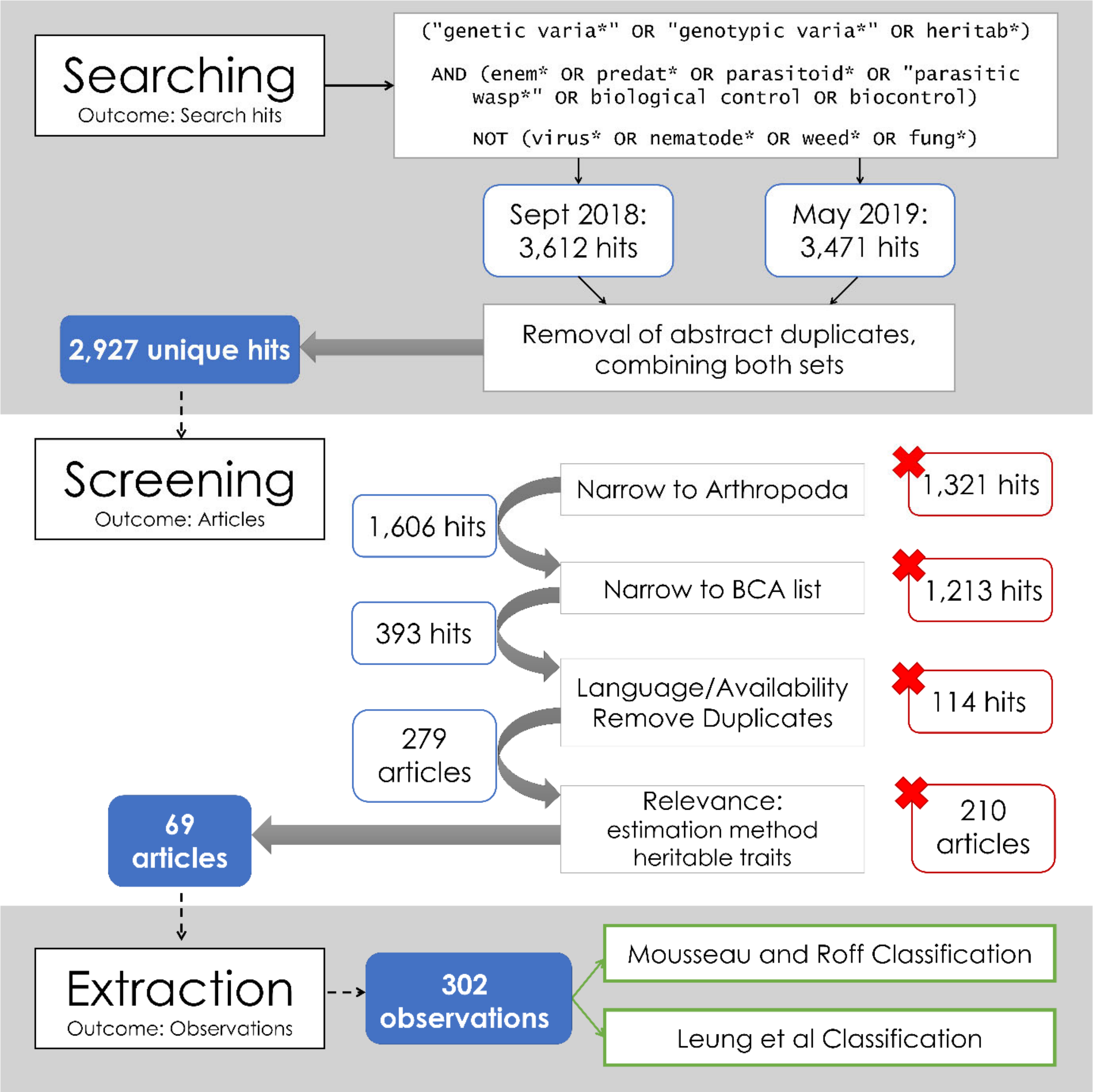

772

773 Figure 1. Flow diagram of the searching, screening, and extraction process used in this
774 systematic review. Classification step is based on fitness components from Mousseau
775 and Roff (Mousseau and Roff, 1987) and aspects of biological control research from
776 Leung et al (Leung et al., 2019)

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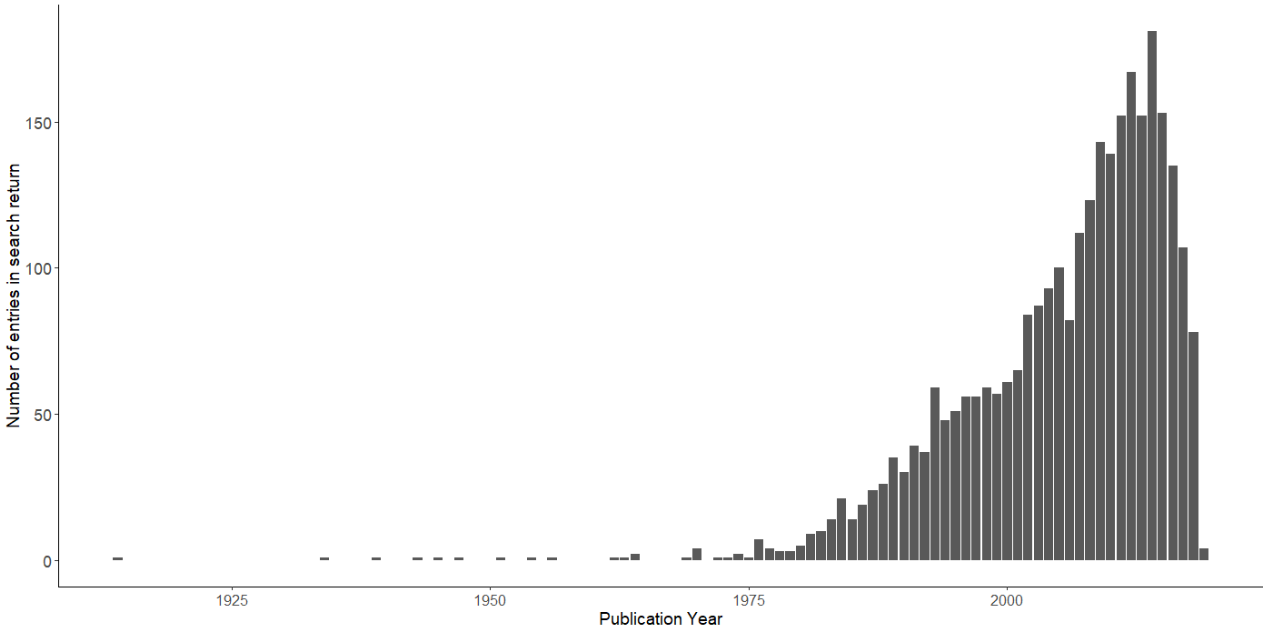
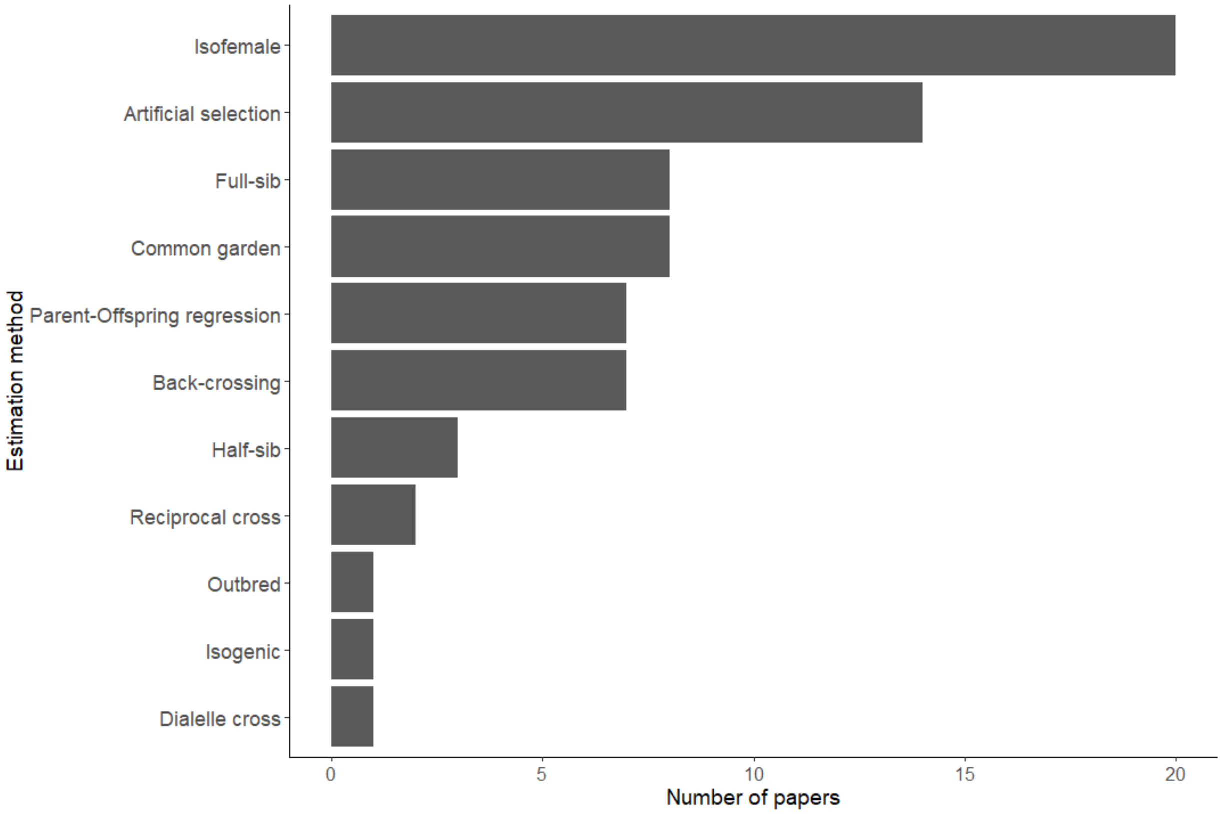


778

779 Figure 2. Initial search returns displayed according to publication year (n = 2, 927).
780 Absent bar indicates 0 search hits for that year.

781



782

783 Figure 3. Estimation methods of extracted papers, reduced to unique species per
784 paper (n = 72).

785

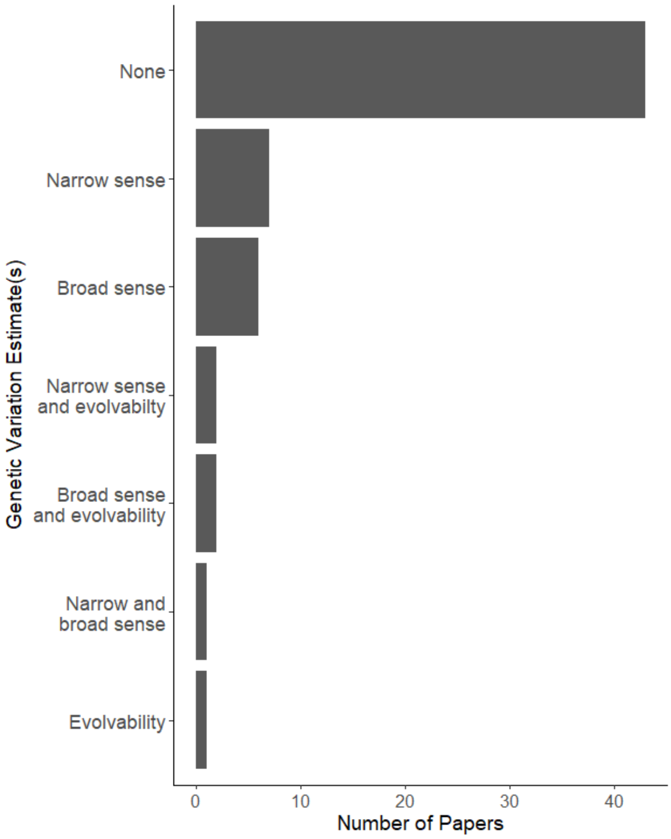


Figure 4. Heritability estimates found in extracted papers (n = 69).

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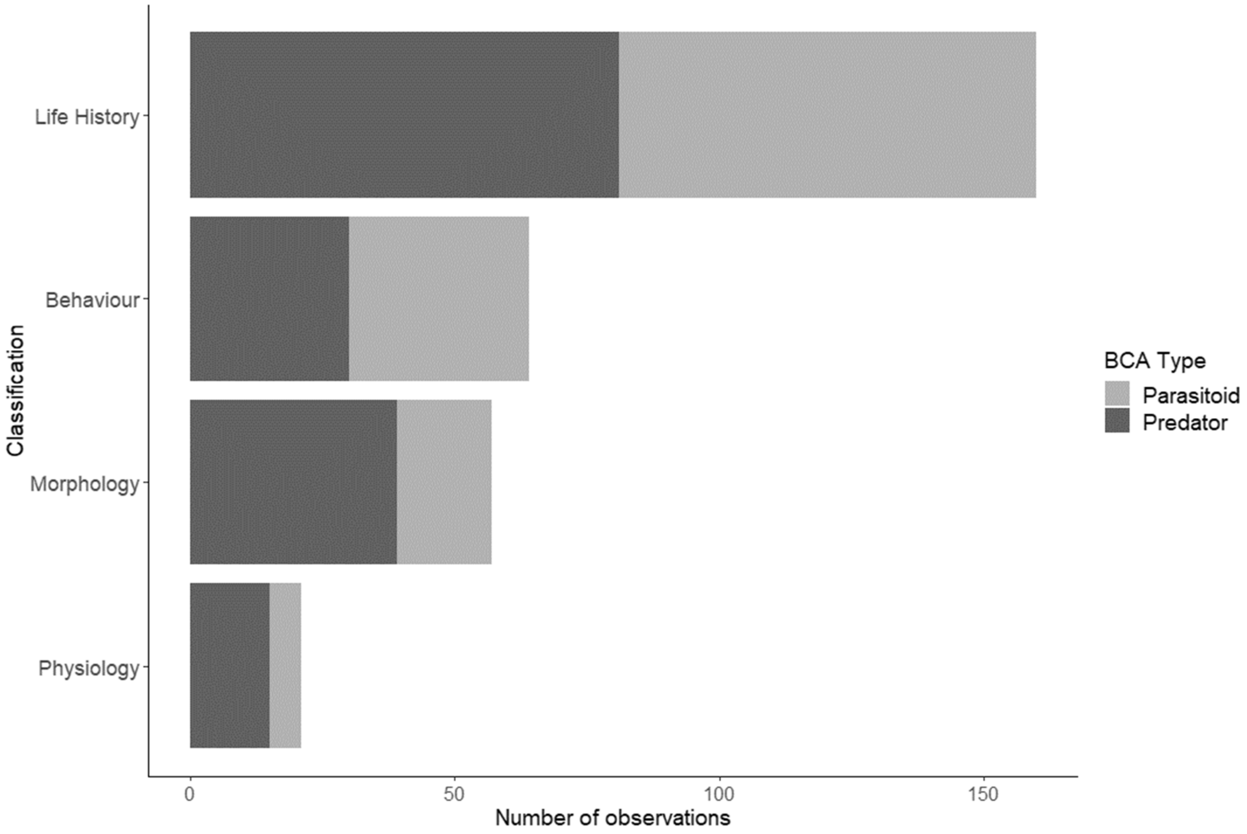

Figure 5. Classification of heritable traits related to fitness, based on Mousseau and Roff (1976), in extracted papers according to BCA type (n = 302).

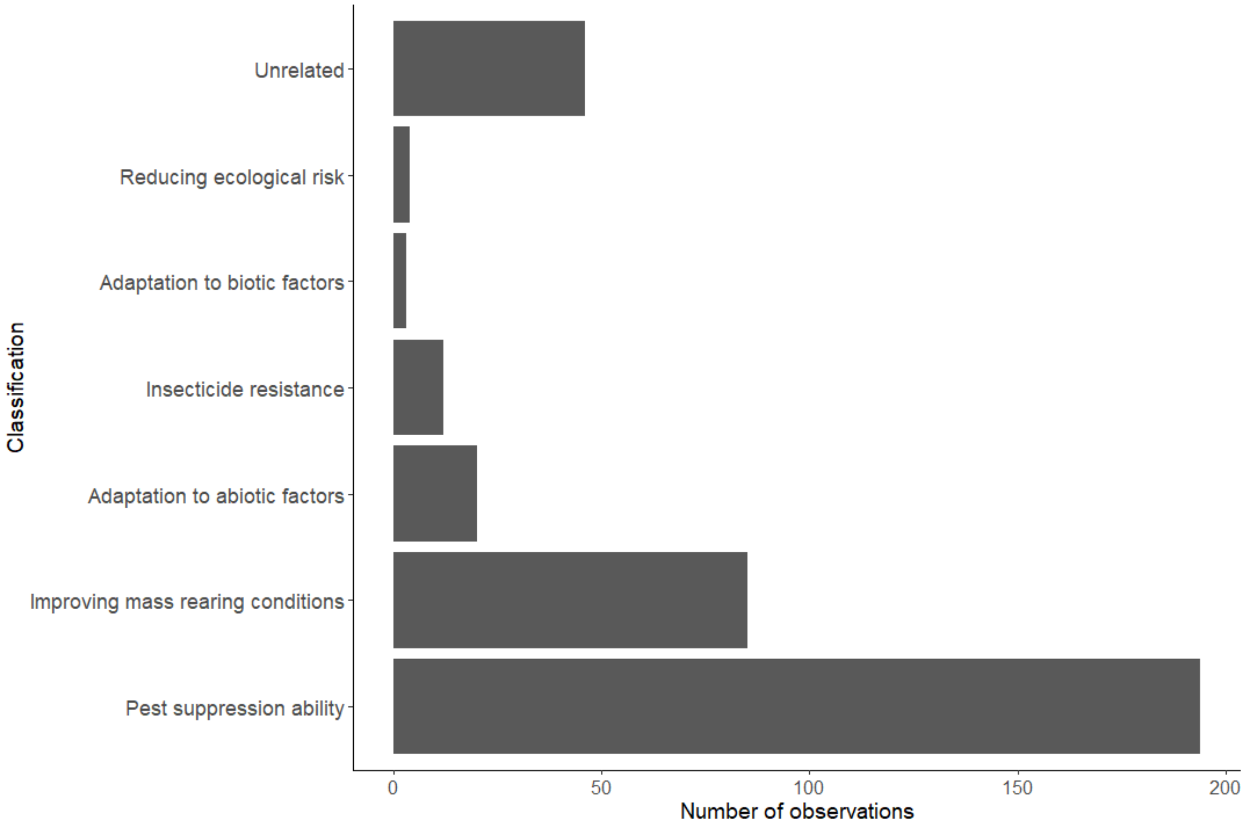

Figure 6. Classification of heritable traits related to importance to biological control research, based on Leung et al (2019), in extracted papers (n = 302).

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Table 1. List of 69 studies examining the genetic heritability of traits in biological control agents (BCAs) that were extracted for this systematic review.

Paper ID[a]	In-text reference	Focal BCA	BCA Type
88	(Hufbauer, 2001)	*Aphidius ervi*	Parasitoid
299	(Guzmán-Larralde et al., 2014)	*Trichogramma pretiosum*	Parasitoid
340	(Bilodeau et al., 2013)	*Aphidius ervi*	Parasitoid
471	(Astles et al., 2005)	*Harmonia axyridis*	Predator
515	(Obrycki et al., 2001)	*Hippodamia convergens*	Predator
525	(Liu and Smith, 2000)	*Trichogramma minutum*	Parasitoid
543	(Grill et al., 1997)	*Harmonia axyridis*	Predator
564	(Rodríguez et al., 1994)	*Trichogramma fuentesi*	Parasitoid
571	(Marples et al., 1993)	*Adalia bipunctata*	Predator
577	(Sequeira and Mackauer, 1992)	*Aphidius ervi*	Parasitoid
768	(Navia et al., 2014)	*Amblyseius largoensis*	Predator
947	(Facon et al., 2011)	*Harmonia axyridis*	Predator
962	(Sayyed et al., 2010)	*Chrysoperla carnea*	Predator
1092	(Fukunaga and Akimoto, 2007)	*Harmonia axyridis*	Predator
1174	(Wang et al., 2004)	*Cotesia glomerata*	Parasitoid
1226	(Thomson and Hoffmann, 2009)	*Trichogramma carverae*	Parasitoid
1286	(Hufbauer and Via, 1999)	*Aphidius ervi*	Parasitoid
1311	(Bennett and Hoffmann, 1998)	*Trichogramma carverae*	Parasitoid
1379	(van Houten et al., 1995)	*Amblyseius barkeri, A. cucumeris*	Predator
1401	(Bruins et al., 1994)	*Trichogramma brassicae*	Parasitoid
1439	(Antolin, 1992)	*Muscidifurax raptor*	Parasitoid
1466	(Legner, 1991a)	*Muscidifurax raptorellus*	Parasitoid
1514	(Legner, 1988)	*Muscidifurax raptorellus*	Parasitoid
1520	(Legner, 1987)	*Muscidifurax raptorellus*	Parasitoid
1528	(Vianen and Lenteren, 1986)	*Encarsia formosa*	Parasitoid
1536	(Parker and Orzack, 1985)	*Nasonia vitripennis*	Parasitoid
1642	(Parreño et al., 2017)	*Lysiphlebus fabarum*	Parasitoid
1675	(Sepúlveda et al., 2017)	*Aphidius ervi*	Parasitoid
1684	(Mansoor et al., 2017)	*Chrysoperla carnea*	Predator
1851	(Kamala Jayanthi et al., 2014)	*Cryptolaemus montrouzieri*	Predator
1868	(Abbas et al., 2014)	*Chrysoperla carnea*	Predator
1899	(Paolucci et al., 2013)	*Nasonia vitripennis*	Parasitoid
1937	(Mansoor et al., 2013)	*Chrysoperla carnea*	Predator
2009	(Wajnberg et al., 2012)	*Trichogramma brassicae*	Parasitoid
2106	(Sandrock et al., 2010)	*Lysiphlebus fabarum*	Parasitoid
2108	(Henry et al., 2010)	*Aphidius ervi*	Parasitoid
2141	(Nachappa et al., 2010)	*Phytoseiulus persimillis*	Predator
2236	(El-Heneidy and Shoeb, 2007)	*Trichogramma evanescens*	Parasitoid
2278	(Pérez-Maluf et al., 2008)	*Leptopilina heterotoma*	Parasitoid
2280	(Pannebakker et al., 2008)	*Nasonia vitripennis*	Parasitoid
2307	(Shuker et al., 2007)	*Nasonia vitripennis*	Parasitoid
2312	(Kamping et al., 2007)	*Nasonia vitripennis*	Parasitoid

Paper ID[a]	**In-text reference**	**Focal BCA**	**BCA Type**
2453	(Wang et al., 2003)	*Cotesia glomerata*	Parasitoid
2465	(Wajnberg et al., 2004)	*Trissolcus basalis*	Parasitoid
2470	(Jia et al., 2002)	*Phytoseiulus persimillis*	Predator
2595	(Maeda et al., 1999)	*Amblyseius womersleyi*	Predator
2601	(Wagner et al., 1999)	*Harmonia axyridis*	Predator
2633	(Lesna and Sabelis, 1999)	*Hypoaspis aculeifer*	Predator
2645	(Mason and Hopper, 1997)	*Aphelinus asychis*	Parasitoid
2657	(Wajnberg and Colazza, 1998)	*Trichogramma brassicae*	Parasitoid
2675	(Gilchrist, 1996)	*Aphidius ervi*	Parasitoid
2689	(Margolies et al., 1997)	*Phytoseiulus persimillis*	Predator
2696	(Sorati et al., 1996)	*Trichogramma brassicae*	Parasitoid
2707	(Henter et al., 1996)	*Encarsia formosa*	Parasitoid
2736	(Holloway et al., 1995)	*Adalia bipunctata*	Predator
2738	(Fleury et al., 1995)	*Leptopilina heterotoma*	Parasitoid
2741	(Henter, 1995)	*Aphidius ervi*	Parasitoid
2755	(Pompanon et al., 1994)	*Trichogramma brassicae, T. cacoeciae*	Parasitoid
2759	(Geden et al., 1992)	*Muscidifurax raptor*	Parasitoid
2763	(Orzack and Gladstone, 1994)	*Nasonia vitripennis*	Parasitoid
2765	(Holloway et al., 1993)	*Adalia bipunctata*	Predator
2781	(Tauber and Tauber, 1992)	*Chrysoperla carnea*	Predator
2782	(Legner, 1993)	*Muscidifurax raptorellus*	Parasitoid
2791	(Legner, 1991b)	*Muscidifurax raptorellus*	Parasitoid
2799	(Orzack et al., 1991)	*Nasonia vitripennis*	Parasitoid
2845	(Boulétreau and Wajnberg, 1986)	*Leptopilina heterotoma*	Parasitoid
2846	(Tauber and Tauber, 1986)	*Chrysoperla carnea*	Predator
3001	(Al-Khateeb et al., 2018)	*Cryptolaemus montrouzieri*	Predator
3007	(Rasmussen et al., 2018)	*Orius majusculus*	Predator

[a] Paper identification number is a unique identifier for each paper and is cross-referenced in Table 2.

Table 2. Extracted observations from 69 studies examining the genetic heritability of life history traits in biological control agents (BCAs), listed according to type of BCA and then by species (n=302).

Type of BCA	Species	Trait of interest as reported	Estimation method	Genetic variation measure	Fitness component[a]	Biological control relevance[b]	Paper ID[c]
Parasitoid	*Aphelinus asychis*	walking speed	common	none	B	7	2645
	Aphidius ervi	body size, female offspring	full-sibling	h^2	L	7	577
		body size, male offspring	full-sibling	h^2	L	7	577
		body size, offspring mean	full-sibling	h^2	L	7	577
		emergence	parent-offspring reg	h^2	L	1	2108
		emergence	parent-offspring reg	h^2	L	1	2108
		emergence	common	none	L	1	340
		female sex ratio	parent-offspring reg	h^2	L	1;4	2108
		female sex ratio	parent-offspring reg	h^2	L	1;4	2108
		fitness	artificial selection	none	L	1	1675
		handling time	artificial selection	none	B	1	1675
		host adaptation	parent-offspring reg	h^2	L	1;3	2108
		host adaptation	parent-offspring reg	h^2	L	1;3	2108
		mass	full-sibling	none	M	1	2675
		ovipositor contact	common	none	B	1	340
		parasitism	half-sibling	h^2, CV_A	L	1	2741
		parasitism	common	none	L	1	1286
		performance breadth	full-sibling	none	P	2	2675
		prey recognition	artificial selection	none	B	1;3	1675
		time to oviposition	artificial selection	none	B	1	1675
		total parasitism	parent-offspring reg	h^2	L	1	2108
		total parasitism	parent-offspring reg	h^2	L	1	2108
		virulence	common	none	P	1	88
		walking speed	full-sibling	none	B	7	2675
	Cotesia glomerata	development time	half-sibling	none	L	7	1174
		efficiency of parasitism	half-sibling	none	L	1	1174
		females per brood	half-sibling	none	L	1;4	1174
		flight orientation	artificial selection	none	B	7	2453

		landing success	artificial selection	none	B	7	2453
Parasitoid	*Cotesia glomerata*	tibia length	half-sibling	none	M	1	1174
	Encarsia formosa	contacts with host	common	none	B	7	2707
		drumming behaviour	common	none	B	7	2707
		encounters	common	none	B	7	2707
		head width	parent-offspring reg	none	M	1;4	1528
		host acceptance	common	none	B	1;3	2707
		host feeding	common	none	B	1	2707
		host rejection	common	none	B	1	2707
		ovariole count	parent-offspring reg	none	L	7	1528
		oviposition acceptance	common	none	B	1	2707
		oviposition posture	common	none	B	7	2707
		successful parasitization	common	none	L	1	2707
	Leptopilina heterotoma	cumulative duration of oviposition	common	none	B	1	2278
		locomotor activity	isofemale	none	B	7	2738
		parasitism rate	common	none	L	1	2845
		probing duration	common	none	B	1	2278
		probing latency	common	none	B	1	2278
		response to olfactory stimuli	common	none	B	1	2278
		survival rate	common	none	L	1	2845
		time to find larvae	common	none	B	1	2278
		time to oviposition	common	none	B	1	2278
	Lysiphlebus fabarum	parasitism	isofemale	H^2	L	1	2106
		wing shape	isofemale	none	M	7	1642
		wing size	isofemale	none	M	7	1642
	Muscidifurax raptor	development time egg to adult	dialelle cross	H^2	L	7	1439
		fecundity	dialelle cross	H^2	L	1;4	1439
		fecundity	parent-offspring reg	h^2	L	1;4	2579
		reproductive lifespan	dialelle cross	H^2	L	1;4	1439
		sex ratio	dialelle cross	H^2	L	1;4	1439
		wing length	parent-offspring reg	h^2	M	7	2579
		wing length	parent-offspring reg	h^2	M	7	2579

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	Muscidifurax raptorellus	eggs laid	backcrossing	none	L	1	1514
		eggs per gregarious oviposition	backcrossing	none	L	1	1514
Parasitoid	*Muscidifurax raptorellus*	eggs per gregarious oviposition	backcrossing	none	L	1	1520
		eggs per gregarious oviposition	backcrossing	none	L	1	2791
		gregarious oviposition	backcrossing	none	L	1	1514
		gregarious oviposition	backcrossing	none	L	1	2782
		gregarious oviposition	backcrossing	none	L	1	1520
		gregarious oviposition	backcrossing	none	L	1	2791
		gregarious oviposition, total	backcrossing	none	L	1	2791
		hosts killed	backcrossing	none	P	1	1520
		hosts parasitized	backcrossing	none	L	1	1520
		longevity females	backcrossing	none	L	1	1520
		parasitism	isofemale	h^2, H^2	L	1	1466
		parasitism	isofemale	h^2, H^2	L	1	1466
		parasitism	backcrossing	none	L	1	2782
		parasitism	backcrossing	none	L	1	2791
		parasitism rate	backcrossing	none	L	1	1514
		sex ratio	backcrossing	none	L	1;4	1520
		sex ratio	backcrossing	none	L	1;4	2791
		total eggs laid	backcrossing	none	L	1	1514
		total eggs laid	backcrossing	none	L	1	2791
		total progeny	backcrossing	none	L	1	1520
	Nasonia vitripennis	copulation duration	half-sibling	h^2, CV_A	B	7	2307
		courtship duration	half-sibling	h^2, CV_A	B	7	2307
		critical photoperiod	isofemale	none	P	1;4	1899
		diapause response	isofemale	none	L	4	1899
		gynandromorphism	isofemale	none	L	7	2312
		lifespan	isofemale	none	L	1;4	1899
		receptivity at 1st courtship	half-sibling	h^2, CV_A	B	7	2307
		receptivity within 10 min	half-sibling	h^2, CV_A	B	7	2307
		second foundress sex ratio	isofemale	H^2	L	1	2280
		sex ratio	isofemale	none	L	1;4	1536

		sex ratio	isofemale	none	L	1;4	2763
		sex ratio	isofemale	none	L	1;4	2799
		single foundress sex raio	isofemale	H^2	L	1;4	2280
Parasitoid	*Trichogramma brassicae*	area searched	isofemale	none	B	1	2657
		body length	isofemale	none	M	1	2696
		body length	outbred	none	M	1	2696
		fecundity	isofemale	none	L	1;4	2696
		fecundity	outbred	none	L	1;4	2696
		head width	isofemale	none	M	1;4	2696
		head width	outbred	none	M	1;4	2696
		hind tibia length	isofemale	none	M	1;4	2696
		hind tibia length	outbred	none	M	1;4	2696
		locomotor activity	isofemale	none	B	7	2755
		male mating	isofemale	none	L	7	2696
		male mating	outbred	none	L	7	2696
		ovigeny index	parent-offspring reg	none	L	1	2009
		reactive distance	full-sibling	none	B	7	1401
		reproductive concentration index	parent-offspring reg	none	L	1	2009
		walking speed	isofemale	none	B	7	2657
		locomotor activity	isofemale	none	B	7	2755
		fecundity	isofemale	H^2	L	1;4	1226
		forewing length	parent-offspring reg	none	M	7	1311
		forewing width	parent-offspring reg	none	M	7	1311
		head width	parent-offspring reg	none	M	1;4	1311
		hind tibia length	parent-offspring reg	none	M	1;4	1311
		hindwing length	parent-offspring reg	none	M	7	1311
	Trichogramma evanescens	developmental period	isofemale	none	L	4	2236
		emergence rate	isofemale	none	L	1;4	2236
		parasitism	isofemale	none	L	1	2236
		sex ratio	isofemale	none	L	1;4	2236
		thermal requirements	isofemale	none	P	2	2236
		host egg color	isofemale	none	P	7	564

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<u>Parasitoid</u>	*Trichogramma evanescens*	emergence	isogenic	H^2	L	1	525
		fecundity	isogenic	H^2	L	1;4	525
		longevity, females	isogenic	H^2	L	1	525
		number female offspring	isogenic	H^2	L	1	525
		number male offspring	isogenic	H^2	L	1	525
		sex ratio	isogenic	H^2	L	1;4	525
		fecundity	isofemale	none	L	1;4	299
		female offspring	isofemale	none	L	1	299
		mean generation time	isofemale	none	L	1;4	299
		reproductive rate	isofemale	none	L	1	299
		sex ratio	isofemale	none	L	1;4	299
	Trissolcus basalis	patch residency	isofemale	none	B	1	2465
		patch-leaving tendency	isofemale	none	B	1	2465
<u>Predator</u>	*Adalia bipunctata*	adaline concentration	parent-offspring reg	none	P	6	2765
		body weight	parent-offspring reg	none	M	1	2765
		growth rate	parent-offspring reg	none	M	4	2765
		reflex fluid	parent-offspring reg	none	P	2	2765
		spot 1 female	parent-offspring reg	none	M	2	2736
		spot 1 male	parent-offspring reg	none	M	2	2736
		spot 2 female	parent-offspring reg	none	M	2	2736
		spot 2 male	parent-offspring reg	none	M	2	2736
		spot 3 female	parent-offspring reg	none	M	2	2736
		spot 3 male	parent-offspring reg	none	M	2	2736
		spot 4 female	parent-offspring reg	none	M	2	2736
		spot 4 male	parent-offspring reg	none	M	2	2736
		wingless	outbred	none	M	1	571
	Amblyseius barkeri	oviposition rate	artificial selection	none	B	1	1379
		predation rate	artificial selection	none	L	1	1379
	Amblyseius cucumeris	eggs laid per female per day	artificial selection	none	L	1	1379
		eggs laid per female per day	artificial selection	none	L	1	1379
		eggs laid per female per day	artificial selection	none	L	1	1379
		eggs laid per female per day	artificial selection	none	L	1	1379

		eggs laid per female per day	artificial selection	none	L	1	1379
		larvae killed per female per day	artificial selection	none	B	1	1379
		larvae killed per female per day	artificial selection	none	B	1	1379
		larvae killed per female per day	artificial selection	none	B	1	1379
		larvae killed per female per day	artificial selection	none	B	1	1379
Predator	*Amblyseius cucumeris*	larvae killed per female per day	artificial selection	none	B	1	1379
		oviposition rate	artificial selection	none	B	1	1379
		predation rate	artificial selection	none	L	1	1379
	Amblyseius largoensis	egg viability	backcrossing	none	L	1;4	768
		eggs laid per female per day	backcrossing	none	L	1	768
		number of eggs	backcrossing	none	L	1	768
		sex ratio	backcrossing	none	L	1;4	768
	Amblyseius womersleyi	dispersal ratio over time	common	none	B	1	2595
		patch choice	common	none	B	1	2595
	Chrysoperla carnea	benzoate resistance	artificial selection	none	P	2	1937
		development time egg to adult	artificial selection	none	L	4	1868
		development time egg to adult	artificial selection	none	L	4	1937
		diapause	full-sibling	none	L	4	2781
		diapause	full-sibling	none	L	4	2846
		eggs laid per female	artificial selection	none	L	1	1868
		eggs laid per female	artificial selection	none	L	1	1937
		emergence rate of healthy adults	artificial selection	none	L	1;4	1868
		emergence rate of healthy adults	artificial selection	none	L	1;4	1937
		fecundity	full-sibling	none	L	1;4	2781
		hatchability	artificial selection	none	L	1;4	1868
		hatchability	artificial selection	none	L	1;4	1937
		larval development time	artificial selection	none	L	4	1868
		larval development time	artificial selection	none	L	4	1937
		larval survival rate	artificial selection	none	L	5	1868
		larval survival rate	artificial selection	none	L	5	1937
		LD50	artificial selection	none	P	5	1684
		LD50	artificial selection	none	P	5	1684
		LD50	artificial selection	none	P	5	1684

		LD50	artificial selection	none	P	5	1684
		net replacement rate	artificial selection	none	L	1;4	1868
		net replacement rate	artificial selection	none	L	1;4	1937
		nondiapause preoviposition period	full-sibling	none	L	1;4	2781
Predator	*Chrysoperla carnea*	number of nextg gen larvae	artificial selection	none	L	1;4	1868
		number of nextg gen larvae	artificial selection	none	L	1;4	1937
		pupal duration	artificial selection	none	L	4	1868
		pupal duration	artificial selection	none	L	4	1937
		pupal weight	artificial selection	none	M	7	1868
		pupal weight	artificial selection	none	M	7	1937
		pupation rate	artificial selection	none	L	7	1868
		pupation rate	artificial selection	none	L	7	1937
		relative fitness	artificial selection	none	L	1	1868
		relative fitness	artificial selection	none	L	1	1937
		resistance alphametrin	artificial selection	h^2	P	5	962
		resistance chlorpyrifos2	artificial selection	h^2	P	5	962
		resistance deltamethrin2	artificial selection	h^2	P	5	962
		resistance lambdacyhalothrin2	artificial selection	h^2	P	5	962
		resistance profenofos2	artificial selection	h^2	P	5	962
		spinosad resistance	artificial selection	none	P	5	1868
	Cryptolaemus montrouzieri	developmental period	artificial selection	none	L	4	3001
		fecundity	artificial selection	none	L	1;4	3001
		female length	artificial selection	none	M	1	3001
		larval developmental time	artificial selection	none	L	4	3001
		prey eaten per day	artificial selection	none	B	1	1851
		prey potential of 3rd instar	artificial selection	none	B	1	3001
		prey potential of female	artificial selection	none	B	1	3001
		reproduction	artificial selection	none	L	1	3001
		survival rate	artificial selection	none	L	1;4	3001
	Harmonia axyridis	abdomen length	full-sibling	H^2, CV_A	M	1	471
		adult development time	artificial selection	h^2, CV_A	L	1	2601
		adult development time	artificial selection	h^2, CV_A	L	1	2601

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Predator	*Harmonia axyridis*	adult mass	full-sibling	H^2, CV_A	M	1	471
		adult size	artificial selection	h^2, CV_A	M	1	2601
		adult size	artificial selection	h^2, CV_A	M	1	2601
		body length	reciprocal cross	CV	M	1	947
		body length	reciprocal cross	CV	M	1	947
		body length	reciprocal cross	CV	M	1	947
		body length	reciprocal cross	CV	M	1	947
		cannibalism rate	artificial selection	h^2, CV_A	B	4	2601
		cannibalism rate	artificial selection	h^2, CV_A	B	4	2601
		development	full-sibling	H^2, CV_A	L	4	543
		development	full-sibling	H^2, CV_A	L	4	543
		development time	full-sibling	H^2, CV_A	L	4	471
		development time egg to adult	reciprocal cross	CV_A	L	4	947
		development time egg to adult	reciprocal cross	CV_A	L	4	947
		development time egg to adult	reciprocal cross	CV_A	L	4	947
		development time egg to adult	reciprocal cross	CV_A	L	4	947
		female reproductive investment	reciprocal cross	CV_A	L	1	947
		female reproductive investment	reciprocal cross	CV_A	L	1	947
		female reproductive investment	reciprocal cross	CV_A	L	1	947
		female reproductive investment	reciprocal cross	CV_A	L	1	947
		hatching time	full-sibling	H^2, CV_A	L	4	471
		larval development time	artificial selection	h^2, CV_A	L	4	2601
		larval development time	artificial selection	h^2, CV_A	L	4	2601
		larval size	artificial selection	h^2, CV_A	M	1	2601
		larval size	artificial selection	h^2, CV_A	M	1	2601
		larval survival to adulthood	reciprocal cross	CV_A	L	7	947
		larval survival to adulthood	reciprocal cross	CV_A	L	7	947
		larval survival to adulthood	reciprocal cross	CV_A	L	7	947
		larval survival to adulthood	reciprocal cross	CV_A	L	7	947
		larval weight	full-sibling	H^2	M	1	1092
		larval weight	full-sibling	H^2	M	1	1092
		orange wing reflectance	full-sibling	H^2, CV_A	M	2	543
		orange wing reflectance	full-sibling	H^2, CV_A	M	2	543

<u>Predator</u>	*Harmonia axyridis*	pronotum width	full-sibling	H^2, CV_A	M	7	471
		pronotum width	full-sibling	H^2, CV_A	M	7	543
		pronotum width	full-sibling	H^2, CV_A	M	7	543
		red wing reflectance	full-sibling	H^2, CV_A	M	2	543
		red wing reflectance	full-sibling	H^2, CV_A	M	2	543
		starvation resistance	reciprocal cross	CV_A	L	1;4	947
		starvation resistance	reciprocal cross	CV_A	L	1;4	947
		starvation resistance	reciprocal cross	CV_A	L	1;4	947
		starvation resistance	reciprocal cross	CV_A	L	1;4	947
		survival rate in quiescent conditions	reciprocal cross	CV_A	L	1;4	947
		survival rate in quiescent conditions	reciprocal cross	CV_A	L	1;4	947
		survival rate in quiescent conditions	reciprocal cross	CV_A	L	1;4	947
		survival rate in quiescent conditions	reciprocal cross	CV_A	L	1;4	947
		thorax length	full-sibling	H^2, CV_A	M	1	471
	Hippodamia convergens	development time egg to adult	backcrossing	none	L	4	515
		elytra size	backcrossing	none	M	2	515
		fecundity	backcrossing	none	L	1;4	515
		fertility	backcrossing	none	L	1;4	515
		pronotum size	backcrossing	none	M	7	515
		sex ratio	backcrossing	none	L	1	515
		survival	backcrossing	none	L	1;4	515
		weight, female	backcrossing	none	M	1	515
		weight, male	backcrossing	none	M	1	515
	Hypoaspis aculeifer	mate choice	backcrossing	none	B	4	2633
	Orius majusculus	basal activity	reciprocal cross	none	B	2	3007
		body size	reciprocal cross	none	M	1	3007
		critical thermal maximum	reciprocal cross	none	P	2	3007
		predation rate	reciprocal cross	none	B	1	3007
		starvation tolerance	reciprocal cross	none	L	1;4	3007
		temperature of maximal activity	reciprocal cross	none	P	2	3007
	Phytoseiulus persimillis	consumption rate	artificial selection	h^2	B	1	2141
		consumption rate	artificial selection	h^2	B	1	2141

Predator	*Phytoseiulus persimillis*	consumption rate	artificial selection	h^2	B	1	2141
		consumption rate	isofemale	h^2	B	1	2470
		conversion efficiency	artificial selection	h^2	L	1	2141
		conversion efficiency	artificial selection	h^2	L	1	2141
		conversion efficiency	artificial selection	h^2	L	1	2141
		dispersal response to prey density	artificial selection	h^2	B	1	2141
		dispersal response to prey density	artificial selection	h^2	B	1	2141
		dispersal response to prey density	artificial selection	h^2	B	1	2141
		eggs laid per female per day avg	artificial selection	none	L	1	2689
		olfactory attraction to *T. urticae* induced plant volatiles	artificial selection	h^2	B	6	2141
		olfactory attraction to *T. urticae* induced plant volatiles	artificial selection	h^2	B	6	2141
		oviposition rate	isofemale	h^2	L	1	2470
		patch residency	isofemale	h^2	B	1	2470
		prey consumption	artificial selection	none	B	1	2689
		prey location	isofemale	h^2	B	1	2470
		residence time	artificial selection	none	B	1	2689

[a] Classification based on Mousseau and Roff (Mousseau and Roff, 1987)

[b] Classification based on Leung et al (Leung *et al.*, 2019)

[c] Paper identification numbers are unique to each paper, and are cross-referenced in Table 1.