

# Quantitative conservation genetics of wild and managed bees

Sheina Koffler<sup>1</sup> · Astrid de Matos Peixoto Kleinert<sup>1</sup> · Rodolfo Jaffe<sup>1,2</sup>

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**Abstract** Quantitative genetic traits provide insights into the evolutionary potential of populations, as heritability estimates measure the population's ability to respond to global changes. Although wild and managed bees are increasingly threatened by the degradation of natural habitats and climate change, risking plant biodiversity and agriculture production, no study has yet performed a systematic review of heritability estimates across the group. Here we help fill this knowledge gap, gathering all available heritability estimates for ants, bees, and wasps, evaluating which factors affect these estimates and assessing the reported genetic correlations between traits. Using a model selection approach to analyze a dataset of more than 800 heritability estimates, we found that heritability is influenced by trait type, with morphological traits exhibiting the highest heritability estimates, and defense and metabolism-related traits showing the lowest estimates. Study system, sociality degree, experimental design, estimation type (narrow or broad-sense heritability), and sample size were not found to affect heritability estimates. Results remained unaltered when correcting for phylogenetic inertia, and when analyzing social bees separately. Genetic correlations between honeybee traits revealed both

positive coefficients, usually for traits in the same category, and negative coefficients, suggesting trade-offs among other traits. We discuss these findings and highlight the importance of maintaining genetic variance in fitness-related traits. Our study shows the importance of considering heritability estimates and genetic correlations when designing breeding and conservation programs. We hope this meta-analysis helps identify sustainable breeding approaches and conservation strategies that help safeguard the evolutionary potential of wild and managed bees.

**Keywords** Bee breeding · Conservation · Genetic correlations · Heritability · Hymenoptera

## Introduction

Wild and managed bees are increasingly threatened by the modification of natural habitats and climate change (Biesmeijer and Roberts 2006; Brown and Paxton 2009; Potts et al. 2010; Kennedy et al. 2013), which poses risks to agricultural production (Gallai et al. 2009) and the maintenance of plant biodiversity (Ollerton et al. 2011). The human-mediated modification of natural habitats can affect the long-term viability of bee populations, fragmenting them, reducing gene flow, and increasing Allee effects (Stephens and Sutherland 1999; Allendorf et al. 2012). For instance, urbanization and agricultural land use have been shown to restrict gene flow in some bee species (Davis et al. 2010; Jha and Kremen 2013; Jha 2015). Likewise, management practices can have a profound influence over genetic differentiation and the maintenance of valuable adaptations to local environmental conditions (De la Rúa et al. 2009; Byatt et al. 2015a). While most studies assessing the conservation status of bee populations have

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✉ Sheina Koffler  
sheina.koffler@usp.br

<sup>1</sup> Department of Ecology, Institute of Biosciences, University of São Paulo, Rua do Matão, 321, São Paulo, SP 05508-090, Brazil

<sup>2</sup> Vale Institute of Technology- Sustainable Development, Rua Boaventura da Silva, 955, Belém, PA 66055-090, Brazil

focused on quantifying bee abundance, species richness or genetic diversity, they have largely neglected quantitative traits. However, quantitative genetic traits provide a direct assessment of the evolutionary potential of populations, and thus their ability to respond to global change (Frankham et al. 2002; Visscher et al. 2008; Zayed 2009).

Quantitative traits are polygenic (determined by a group of genes) and exhibit complex inheritance patterns (Frankham et al. 2002). To measure trait inheritance, heritability estimates are calculated as the ratio of genetic variance to total phenotypic variance (Falconer and Mackay 1996). Heritability estimates thus represent a proportion, and range between 0 (indicating no genetic variance, or traits which are solely affected by the environment) and 1 (for traits regulated exclusively by genetic variance, which are unaffected by the environment). While narrow sense heritability indicates the proportion of the phenotypic variance attributable to additive genetic variance, broad sense heritability is estimated as the ratio between genotypic variance (additive, dominance and epistasis effects) and total phenotypic variance. Traits with high heritability estimates provide a higher ability to respond to selection, as a large range of phenotypes will be available for selection to act upon. In contrast, traits showing low heritabilities have a more restricted response to selection.

Fitness-related traits generally exhibit low heritability estimates, because the fixation of advantageous traits reduces additive genetic variance (Frankham et al. 2002; Visscher et al. 2008). For example, life-history traits in 75 species from wild and outbred populations were found to show much lower heritabilities than morphological traits (Mousseau and Roff 1987). Such fitness-related traits are of primary conservation interest, because they indicate the ability of populations to respond to selection (Frankham et al. 2002). Additionally, fitness-related traits show higher dominance genetic variance, which increases the susceptibility of inbreeding (Frankham et al. 2002). Populations that face severe declines are under strong genetic drift, which reduces genetic diversity, increases inbreeding, and may eventually erode heritability of fitness-related traits. However, heritability estimates may not be directly related to genetic diversity, as traits can show a low (or high) genetic variance regardless of population-wide genetic diversity (Reed and Frankham 2001). Integrating a population's response to selection and traits heritability is thus essential to understand adaptive response in changing environments (Hendry et al. 2003).

A potential application of quantitative genetic studies for the conservation of wild bee populations is the estimation of heritability for disease resistance, as different species are currently threatened by the spillover of pathogens from managed populations (Sachman-Ruiz et al. 2015). Quantitative genetic variability is also the basis of breeding initiatives, which select and enhance traits of interest. In honeybees, for instance, quantitative genetic studies can

help breed for traits like resistance to *Varroa jacobsoni* (Harbo and Harris 1999), honey production, colony defensive behavior (Bienefeld et al. 2007). Using heritability estimates, Harbo and Harris (1999) identified four potential traits for breeding to increase mite resistance. Also relying on quantitative genetic approaches, Bienefeld et al. (2007) increased the selection response to honey production from 0.04 to 0.54% per year, and to colony defense behavior from 0.03 to 0.62%. On the other hand, body size of *Osmia lignaria* (a solitary bee used in commercial pollination) exhibited a low heritability, indicating that breeding to modify body size is unlikely to yield the desired results in this species (Tepedino et al. 1984). These examples illustrate how conservation and breeding efforts can benefit from quantitative genetic studies.

In the Hymenoptera (ants, bees, and wasps), quantitative genetic studies pose important challenges, due to the haplodiploid sex determination system and complex genetic architecture (Oxley and Oldroyd 2010). Early initiatives adapted existing methods and protocols available for diploid species (Rinderer 1977; Oldroyd and Moran 1983; Moritz 1985). More recent developments include protocols for narrow sense heritability estimations (Liu and Smith 2000) and the use of BLUP models (Best Linear Unbiased Predictors) for estimating breeding values (Bienefeld et al. 2007; Gupta et al. 2013). Although a body of studies have used quantitative genetic approaches for breeding purposes (Harbo 1992; Conte et al. 1994; Brascamp et al. 2016), no previous efforts have been made to systematically review heritability estimates across the group and assess their implication for bee conservation. In addition to heritability estimates, genetic correlations between traits are important to gain a more complete understanding of inheritance, as multiple traits respond simultaneously to selection.

Here we perform the first systematic review of heritability estimates across the Hymenoptera. Our main aim was to assess how natural and artificial selection operate across multiple traits, and how bee breeding practices could cause a reduction in evolutionary potential. We first evaluate how different factors influence heritability estimates, and then compare estimates and genetic correlations among different traits across social bees. We predicted that heritability estimates would be affected by trait type, study system, sociality degree, experimental design, estimation type (narrow or broad-sense heritability), and sample size; and that similar traits would show positive correlations.

## Materials and methods

We performed a systematic review on available studies reporting heritability estimates across the Hymenoptera. Three online databases were accessed (Google Scholar,

Scopus, and Web of Science), using different combinations of key words (heritability, quantitative genetics, social insects, bees, ants, wasps). Each study was checked for heritability estimates and a library of selected studies was prepared. Articles cited in the selected studies were also included in our dataset. Overall, we collected information from 90 studies (Supp. Table 1). For each study we retrieved: (a) study system (ant, bee or wasp); (b) species; (c) sociality degree (social or solitary); (d) experimental design (diallel cross, ratio between genetic and total phenotypic variance, breeder's equation, sibling analysis, and parent-offspring regression); (e) estimate type (narrow or broad-sense heritability); (f) number of families employed (number of colonies for social species or number of maternal lineages for solitary species); (g) number of individuals analyzed; (h) trait category (behavior, communication, defense, fertility, metabolism, morphology, and colony productivity); and (i) analyzed trait. Heritability estimates were classified as narrow-sense when the study design allowed additive genetic variance estimation, following the methods discussed in Liu and Smith (2000). In addition, we also considered as narrow-sense the estimates obtained by regression methods among generations, corrected by the relatedness coefficients; as well as realized heritability estimates, which are an indirect method of measuring additive genetic variance. The ratio between genetic and total phenotypic variance (henceforth G/T estimation) was always classified as broad-sense heritability since it does not allow differentiating additive variance from dominance or epistasis effects. When sample sizes (number of families or individuals) were given in intervals, we conservatively considered the lower number. In order to reduce the number of trait types in our dataset, we assigned them to seven categories: Behavior, Communication, Defense, Fertility, Metabolism, Morphology, and Colony productivity (Table 1).

Negative heritability estimates and estimates above 1 were excluded from the analyses, since they reflect negative genetic variances or limitations related to inbreeding. In order to identify which factors influenced heritability estimates across the Hymenoptera, we ran linear mixed effects models with the arcsine-transformed heritability as response variable and species as a random factor. All factors which could potentially affect heritability estimates (study system, sociality degree, experimental design, estimate type, number of families, number of individuals, and trait category) were included as predictors. Because some of these factors contained missing data and small sample sizes in certain categories, we could not fit a full model containing all predictors. Instead, we ran simple models using complete cases datasets, containing a single predictor. Models with individual predictors were contrasted to null models (without the predictor), using likelihood ratios

tests (LRT) with  $\alpha = 0.05$ . We then built a full model containing the predictors showing a significant influence on heritability estimates. This full model was compared to reduced models without each predictor (also employing LRT), until we reached the best model, where the exclusion of any predictor significantly decreased the model's log-likelihood. We also tested whether including a variance structure improved the model's likelihood or not, using a constant variance structure to allow different variances among categories. Models with a variance structure were compared to homoscedastic models using LRT. To account for phylogenetic dependence among species, we ran phylogenetic controlled regressions, using a tree constructed with the species in our dataset (Quicke and van Achterberg 1900; Downton and Austin 1994; Cameron et al. 2007; Hughes et al. 2008; Munro et al. 2011; Danforth et al. 2013) (Fig. S1, see also the supplementary R file with the tree). Phylogenetic relationships among corbiculate bees were retrieved from Danforth et al. (2013), multiple observations from the same species were included as polytomies, and branch lengths were considered equal (length = 1). We then constructed generalized least squares models controlling for phylogenetic effects (Pagel 1999), using the arcsine-transformed heritability as response variable and the predictors contained in the best linear mixed models. Both linear mixed models and phylogenetic controlled regressions were implemented using the full dataset and a data subset including social bees only. All analyses were performed in R, using the *lme4* (Bates et al. 2014) and *nlme* (Pinheiro et al. 2016) packages. The R packages *ape* (Paradis et al. 2004), *geiger* (Harmon et al. 2008), and *phytools* (Revell 2012) were used to construct and manipulate the phylogenetic tree. Plots were produced with the package *ggplot2* (Wickham 2009).

Genetic correlations between traits were also assessed and correlation coefficients for *Apis mellifera* traits were compiled and grouped in categories (Table 1), since this species exhibited most of the available information on genetic correlations (Supp. Table 2). As most studies did not present significance tests for genetic correlation coefficients, we included all coefficients in our dataset. Correlation coefficients below  $-1$  and above  $1$  were discarded from the analysis, because they do not fit in the parameter space of coefficients of correlation (Wielewski et al. 2014) and may be related to problems in the covariance estimation.

## Results

We gathered a total of 806 heritability estimates for 32 Hymenoptera species (Supp. Table 1). Ants were the worst represented group, with 7% of the estimates, followed by

**Table 1** Classification of the analyzed traits

Trait category	Trait type	Traits
Behavior	Leaning (PER)	Learning (proboscis extension reflex), resistance of the conditioned response to extinction
	Number of matings	Estimated and effective number of matings
Communication	Colony defense	Colony defense, honey robbing
	Reaction to alarm pheromone (time)	Time to react to alarm pheromone (laboratory essays, field essays), time to first sting, time for clustering
	Reaction to alarm pheromone (number of bees)	Number of bees reacting to alarm pheromone (laboratory essays, field essays), number of stings in target
	Reaction to alarm pheromone (oxygen consumption)	
	Alarm pheromone production	Production of isopentyl acetate, 1-hexanol, 2-heptyl acetate, octyl acetate, 2-nonyl acetate, 2-heptatone
Defense	Worker dominance	Trophallactic dominance, 9-ODA in mandibular gland
	Kin recognition	
	Hygienic behavior	Hygienic behavior after 24 h, 48 h, 72 h, towards Varroa-infested brood cells
	Mite population	Final mite population, mites on adult bees, mites on brood cells
Fertility	Mite reproduction	Total mite reproduction rate, effective mite reproduction, suppression of mite reproduction
	Grooming behavior	Grooming behavior, physical damage to mites (total, dents in body, broken legs or bodies)
	Immune response	Immune gene expression, innate immune response
Metabolism	Number of ovarioles	
	Ovary development	
	Oviposition	Number of eggs laid, days of oviposition
	Worker development	Total development, duration of uncapped stage, duration of postcapping stage
Morphology	Queen development	Duration of queen postcapping stage
	Drone maturation rate	Age at the onset of flight, initial locomotor activity (light and dark)
	Worker longevity	
	Cold resistance	
	Oxygen consumption	
	Worker pupal weight	
	Male size	
	Color pattern	Worker, drone and queen color patterns
	Proboscis length	
	Forewing size	Forewing length and width, wing venation (L1, L2, cubital A, cubital B)
Colony productivity	Forewing angles	Forewing angles (29, 30, 31, 32, 33, 34, 35, 36, 38, 39)
	Cubital index	
	Hindwing size	Hindwing length, hindwing width, hindwing area
	Number of hamuli	
	Wax mirror morphology	Wax mirror length, wax mirror width, distance between wax mirrors
	Third sternum length	
	Hind leg morphology	Leg area and length, tibia length, femur area and length, basitarsis length and width, metatarsus length and width, length of corbicula hairs
	Sting morphology	Sting length, stylet length, bulb length, maximum width of bulb, lancet length, height of the valve of right lancet, number of tooth barb of sting
	Spem length	Individual sperm length, mean sperm length
	Colony development	Colony weight, weight gain, spring development (score)
	Colony population	Brood production, brood viability, number of bees covering combs
	Honey production	Honey production (annual or seasonal), number and dimensions of honey pots
Wax production		
Propolis production		

**Table 1** continued

Trait category	Trait type	Traits
	Royal jelly production	Royal jelly production (per colony, per cup), larvae acceptance
	Foraging success	Hoarding behavior, syrup collection rate, pollen hoarding, number and dimensions of pollen pots, sunflower pollen collection, avocado foraging, allometry coefficient between glossa and wing lengths
	Colony aggressiveness	Aggressiveness or calmness during colony inspection (score)
	Swarming	

wasps (15%) and bees (78%). Solitary species were well represented in wasps (61% of the estimates); while in bees few estimates were found for solitary species (n = 8, *Osmia lignaria* and *Megachile rotundata*). Social bees included *Apis mellifera*, four bumblebee species (*Bombus huntii*, *B. occidentalis*, *B. rufocinctus*, and *B. terrestris*), and two stingless bees (*Melipona quadrifasciata* and *M. scutellaris*). Broad-sense estimates were far more common (78%) than narrow-sense estimates.

Trait category was the best predictor of heritability (LRT:  $\chi^2 = 100.22$ ,  $p < 0.001$ , Table 2), with morphological traits exhibiting the highest estimates and defense and metabolism-related traits showing the lowest estimates (Table 3; Fig. 1). None of the other tested predictors (study system, sociality, experimental design, estimate type, number of families, and number of individuals), nor a variance structure in the best model were found to improve the model’s likelihood (LRT: 3.37,  $p = 0.76$ ). Variance was similar for broad and narrow-sense estimates (the inclusion of a variance structure did not improve the model’s log-likelihood of a model containing trait category and estimate type as predictors; LRT: 1.75,  $p = 0.17$ , Fig. S2). Results remained unaltered when controlling for phylogenetic effects (LRT:  $\chi^2 = 86.12$ ,  $p < 0.001$ , Tables 2, 3). Additionally, the same results were found when analyzing social bees only (not accounting for phylogenetic effects LRT:  $\chi^2 = 99.41$ ,  $p < 0.001$ , accounting for phylogenetic effects LRT:  $\chi^2 = 152.60$ ,  $p < 0.001$ , Tables 2, 3; Fig. 2).

Genetic correlations between honeybee traits are shown in Fig. 3. Traits related to the same trait category usually

exhibited positive genetic correlations, with the exception of communication traits. In general, morphological traits were positively correlated. Although sting pheromones were positively correlated, there was a negative association between sting pheromones and mandibular gland pheromones. Honey production and hoarding behavior were negatively correlated to hygienic behavior and mite presence. In addition, honey production also exhibited negative genetic correlations with colony aggressiveness. Positive genetic correlations were found between colony aggressiveness and swarming, hygienic behavior and propolis production, mite presence and propolis production, honey production and propolis production, defense and comb cell size, and defense and longevity.

### Discussion

Heritability was best explained by trait category, with morphological traits showing the highest heritability estimates and defense and metabolism-related traits showing the lowest. Our collection of available heritability estimates for Hymenoptera species revealed that social bees, and particularly honeybees, are the best represented group. Additionally, genetic correlations between honeybee traits revealed both positive coefficients, usually for similar traits, and negative coefficients.

Even though the main Hymenoptera groups (ants, bees and wasps) were represented in our dataset, there was a strong bias towards honeybee studies. This was expected since honeybees are key managed pollinators and an

**Table 2** Best models describing heritability

Response (Dataset)	N	Model	Predictor	$\chi^2$	d.f.	P value
Heritability (Hymenoptera species)	620	LMM	Trait category	100.22	6	<0.001
Heritability (Hymenoptera species)	635	GLS controlling for phylogenetic effects <sup>a</sup>	Trait category	86.12	6	<0.001
Heritability (social bee species)	444	LMM	Trait category	99.41	4	<0.001
Heritability (social bee species)	476	GLS controlling for phylogenetic effects <sup>b</sup>	Trait category	152.60	6	<0.001

N is the number of observations of each model, while the p-values and degrees of freedom (d.f.) refer to the likelihood ratio tests (using a  $\chi^2$  test statistic), in which the full model was compared to a reduced model without trait category

<sup>a</sup>  $\lambda = 0.34$ ; <sup>b</sup>  $\lambda = -0.05$

**Table 3** Parameter estimates for the best models describing heritability

Response (dataset)	Model	Predictor (trait category)	Estimate	SE	d.f.	P-value
Heritability (Hymenoptera species)	LMM	Behavior	−0.079	0.054	601.9	0.14
		Communication	−0.008	0.031	611.2	0.79
		Defense	−0.195	0.028	612.1	<0.001
		Fertility	−0.110	0.036	522	0.002
		Metabolism	−0.223	0.037	599.4	<0.001
		Productivity	−0.152	0.019	609.7	<0.001
Heritability (Hymenoptera species)	GLS controlling for phylogenetic effects	Behavior	−0.093	0.053	–	0.08
		Communication	−0.012	0.030	–	0.70
		Defense	−0.165	0.027	–	<0.001
		Fertility	−0.093	0.035	–	0.008
		Metabolism	−0.217	0.037	–	<0.001
		Productivity	−0.136	0.019	–	<0.001
Heritability (social bee species)	LMM	Communication	−0.010	0.034	439	0.76
		Defense	−0.219	0.029	439	<0.001
		Metabolism	−0.223	0.045	439	<0.001
		Productivity	−0.154	0.020	439	<0.001
Heritability (social bee species)	GLS controlling for phylogenetic effects	Behavior	−0.141	0.063	–	0.03
		Communication	−0.009	0.035	–	0.80
		Defense	−0.172	0.034	–	<0.001
		Fertility	−0.150	0.043	–	<0.001
		Metabolism	−0.202	0.039	–	<0.001
		Productivity	−0.124	0.027	–	<0.001

Estimates for each trait type are given with morphological traits as comparison base (the negative estimates values indicate that morphological traits exhibited the highest estimates). Trait types with low sample sizes ( $n < 8$ ) were excluded from the analyses. SE is the standard error, d.f. the degrees of freedom, and P-values were computed using the Satterthwaite approximation (*lmerTest* package)

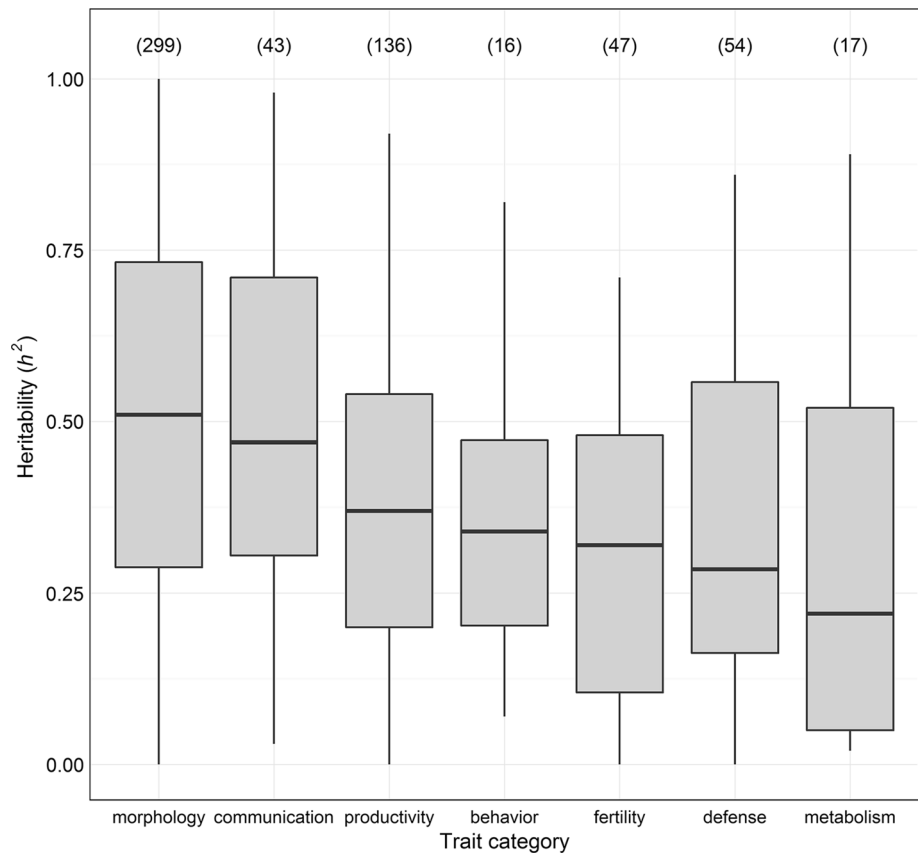
important model system for genetic studies (Oxley and Oldroyd 2010; Evans et al. 2013). However, we highlight the underrepresentation of other social and solitary bees, which are also important providers of pollinator services (Nunes-Silva et al. 2013; Giannini et al. 2014) and may be experiencing population declines (Brown and Albrecht 2001; Kennedy et al. 2013). In addition, the commercial use of stingless bees has been highlighted as a key tool to achieve sustainable rural development, although management practices are still less developed than in apiculture (Jaffé et al. 2015; Koffler et al. 2015). The lack of quantitative genetic studies in bees other than honeybees thus hinders breeding and conservation efforts.

Estimate type did not improve our model's likelihood, indicating that studies calculating narrow-sense heritability obtained similar estimates to those computing broad-sense estimates. Narrow-sense heritability estimates were less represented in our dataset, perhaps because their estimation requires a more complex experimental design. Narrow-sense estimates usually involve more than one generation (realized heritability in breeder's equation, parent-offspring regression and diallel crosses), thus requiring longer studies. Since broad-sense estimates are based on total genetic

variance, they are expected to be more variable than narrow-sense estimates, which only include additive genetic variance (Falconer and Mackay 1996; Bennett and Hoffmann 1998; Hoffman et al. 2008; Kovacs et al. 2009; Stürup et al. 2011). However, our results show that variance was similar for broad and narrow-sense estimates.

Our dataset shows there are numerous methods employed to estimate heritability, still a subject of debate (Fjerdingstad 2005). Although experimental design was not detected as a factor influencing heritability estimates, a separate analysis of the best represented trait in our dataset (honey production in honeybees) revealed that GT estimates were higher than those obtained through parent-offspring regression. These results thus indicate that estimation method can influence heritability, even though other confounding factors and low sample sizes might have masked its effects when analyzing our full dataset. Our study thus highlights the need to standardize methodological approaches to estimate quantitative genetic parameters in bees (Liu and Smith 2000; Bienefeld et al. 2007). A recent review of heritability estimates in wild vertebrates showed that estimates obtained using the animal model were lower and more precise than other methods (sib-

**Fig. 1** Heritability estimates for seven trait categories for all Hymenoptera species. While median values are represented by the lines inside boxes, which span the first and third quartiles, sample sizes are provided in brackets



analyses, parent-offspring and grandparent-offspring regressions), suggesting that future studies should embrace this new approach, which integrates different relatedness degrees and common environment dependence (Postma 2014).

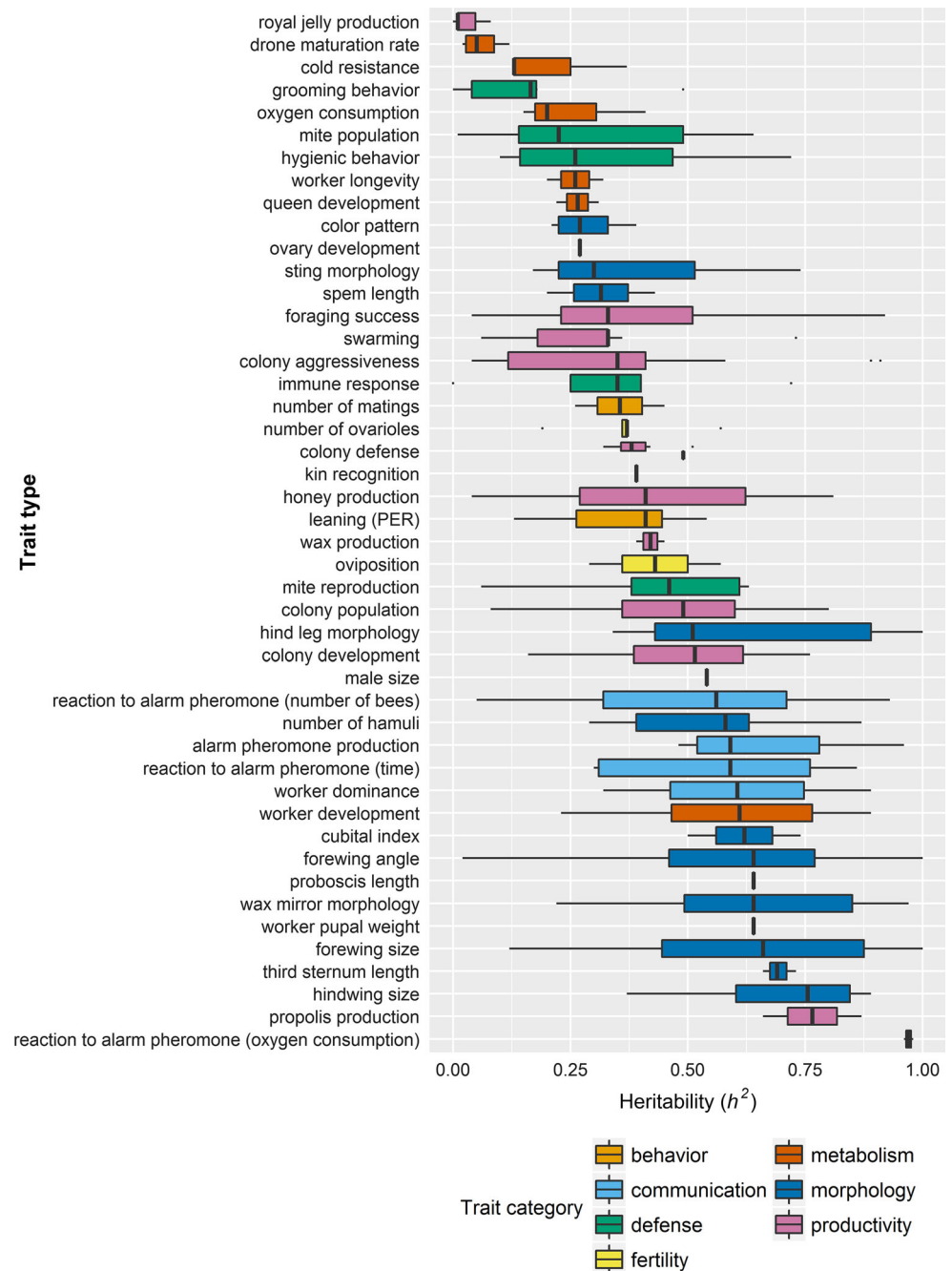
We found a large variation in heritability estimates within traits and trait categories (Figs. 1, 2), although variance did not vary among categories. Such variation could be related to temporal or environmental changes, since heritability values estimated in the same population at different times may vary (Fjerdingstad 2005; Kovacs et al. 2009). Higher heritability estimates are usually found under more favorable conditions (Charmantier and Garant 2005). In addition, because heritability is a population measure (Visscher et al. 2008), the investigation of different populations of the same species may provide different heritability estimates. Population-level variation in heritability suggests that each population comprises a different genetic repository worthwhile preserving (Collins et al. 1984; Oldroyd et al. 1991).

Trait category was the best predictor for heritability across the Hymenoptera as well as within social bees. Many social bee traits exhibited medium to high heritability estimates, indicating large potential for breeding and genetic improvement. Morphological traits showed the highest heritability estimates, a result expected for traits

not directly related to fitness (Falconer and Mackay 1996; Frankham et al. 2002; Visscher et al. 2008; Postma 2014). Colony productivity indicators (such as honey production, colony population, and foraging success) showed a high heritability, and thus a great potential for genetic improvement. Defense and metabolism traits showed the lowest heritability estimates, which suggest their close relation with fitness. Our work thus suggests that breeding programs focused on traits directly related to disease resistance (as hygienic behavior) may only lead to a modest increase in trait expression.

Breeding initiatives in social bees should also consider genetic correlations between traits, since they can enhance or impair breeding outcomes (Oxley and Oldroyd 2010). In honeybees, similar traits usually showed positive genetic correlations, suggesting the same mechanism of control. Communication traits such as response to alarm pheromones, however, presented negative correlations, indicating trade-offs. The positive genetic correlations observed reveal that breeding may simultaneously decrease colony aggressiveness and swarming behavior, increase hygienic behavior and propolis production, increase honey production and propolis production, and increase communication and longevity. Breeding attempts focused on these traits are thus expected to generate healthier and more productive colonies, although they could quickly deplete

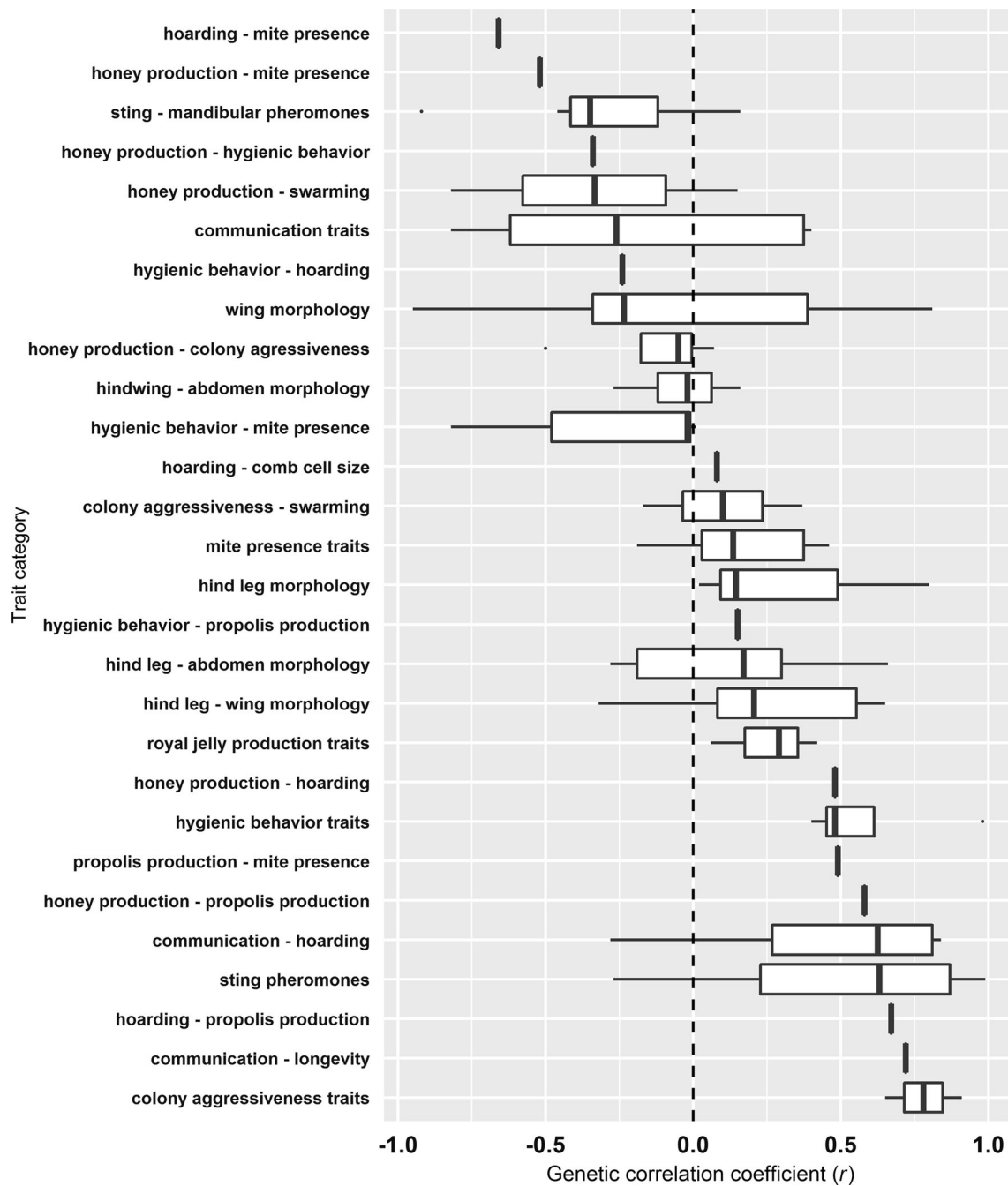
**Fig. 2** Heritability estimates for social bee traits. While median values are represented by the *lines inside boxes*, which span the first and third quartiles, trait categories are represented by different colors



genetic variation of low heritability traits (see discussion below). On the other hand, negative genetic correlations may indicate trade-offs and selection acting on opposite directions, so that breeding efforts may not lead to colonies simultaneously expressing all desirable traits. For example, breeding for increase hygienic behavior would reduce honey production. In addition, negative genetic correlations were found between worker and queen effects in traits such wax and honey production (Bienefeld and Pirchner 1990); hygienic behavior (Costa-Maia et al. 2011); and honey yield and colony behavior (Brascamp et al. 2016).

By targeting such negatively-correlated traits, breeding efforts could also help maintain genetic variance in the population, as breeding optima are likely to differ for each trait. Considering both heritability and genetic correlations may thus provide valuable information for breeding programs, regarding the effectiveness of genetic improvement efforts, and the conservation of genetic variance in the traits of interest. In addition, the identification of quantitative trait loci (QTLs) and recent genomic approaches may confirm genetic linkages between traits, measure the strength of the association, and identify epistasis effects





**Fig. 3** Coefficients of genetic correlations between *Apis mellifera* traits. The dashed line shows the null coefficient, so negative correlations are exhibited left, and the positive correlations right.

Median values are represented by the lines inside the boxes, which span the first and third quartiles

among genes, providing a more accurate pattern of multiple trait inheritance (Jensen et al. 2014).

Even though breeding has been highlighted as a long-term sustainable solution for the recent bee conservation challenges (Niño and Cameron Jasper 2015), its possible negative effects must also be considered, which include the loss of genetic variance, an increase in the level of inbreeding, outbreeding depression, introgression, and the

loss of local adaptations to environmental conditions (Meixner et al. 2010; Oxley and Oldroyd 2010; Allendorf et al. 2012; Büchler et al. 2014; Niño and Cameron Jasper 2015). It is thus important to promote best practices for breeding programs (Byatt et al. 2015b; Niño and Cameron Jasper 2015) if additive genetic variance is to be maintained in both wild and managed populations. Our work highlights the need to monitor additive genetic variance in

fitness-related traits, a practice that is yet uncommon and not sufficiently emphasized by current breeding initiatives (Meixner et al. 2010; Oxley and Oldroyd 2010; Niño and Cameron Jasper 2015). Future conservation programs could also incorporate quantitative genetic information, for example when choosing traits of special interest for reintroduction in areas where genetic variance has already been depleted. The protection of wild populations containing a large genetic variance for specific traits of interest may also help safeguard genetic stocks for future breeding or conservation efforts (Frankham et al. 2002; Zayed 2009).

In places with large wild or feral honeybee populations (like Africa, South America and Australia), breeding efforts are unlikely to deplete genetic variation in wild populations. However, in places like Europe, where wild honeybee populations have nearly gone extinct (Jaffé et al. 2010), breeding could have a significant influence over the long-term maintenance of genetic variation for desirable traits. Likewise, long-term breeding efforts relying on closed-population systems, instrumental queen insemination, and few sources of queen lineages, which favors inbreeding (Chapman et al. 2008; Meixner et al. 2010; Niño and Cameron Jasper 2015), need to be especially careful to avoid the depletion of additive genetic variance of important fitness-related traits. We posit that some of the reported bee declines (Goulson et al. 2015) could be related to low genetic variance for fitness-related traits, and thus highlight the need for future studies specifically addressing this issue.

Our study summarizes all available heritability estimates for Hymenoptera species, providing a baseline for breeding and conservation studies, and identifying knowledge gaps and research needs. Quantitative genetic studies may contribute significantly towards the conservation of wild and managed bees, as our study shows the importance of considering heritability estimates and genetic correlations when designing breeding and conservation programs. Finally we emphasize the importance of extending quantitative genetic studies beyond honeybees, to address other ecologically and economically important but yet understudied bees. We hope this meta-analysis helps identify sustainable breeding approaches and conservation strategies that help safeguard the evolutionary potential of wild and managed bees.

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