

Behavioral Syndromes in Social Insects

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ABSTRACT

Behavioral syndromes -- the consistent covariation of behavioral traits across contexts and individuals, producing repeatable behavioral types or personalities -- have been widely documented in solitary animals but their expression in social insects, where individual behavior is embedded within the collective behavior of a superorganism colony, represents a fundamentally different and less well-understood level of organisation. This study presents the most comprehensive comparative analysis of behavioral syndromes in social insects yet conducted, quantifying individual and colony-level behavioral repeatability across 247 colonies from 18 species spanning ants, bees, wasps, and termites, using a standardised multi-context behavioral assay battery repeated across four seasonal time points per colony. Individual-level behavioral syndromes were confirmed in 14 of 18 species (78%): individuals consistently classified as bold-active or cautious-inactive across foraging, nest defence, and exploration contexts (mean repeatability $r = 0.47 \pm 0.14$). Colony-level syndromes were confirmed in all 18 species (100%; $r = 0.64 \pm 0.12$). Colony syndrome predicted colony performance: bold colonies showed 34.7% higher food acquisition but 18.4% higher worker mortality under predator exposure, confirming a boldness-risk trade-off at the colony level. Queen genotype explained 28.4% of colony syndrome variance, confirming a heritable genetic component to colony behavioral type.

Keywords: behavioral syndromes; animal personality; social insects; colony personality; repeatability; Hymenoptera; foraging boldness; collective behavior

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1. Introduction

1.1 Animal Personality and Behavioral Syndromes

The recognition that individual animals consistently differ from one another in behavioral tendencies -- that some individuals are consistently bolder, more exploratory, or more aggressive than others regardless of context -- has transformed behavioral ecology over the past two decades. The term 'behavioral syndrome' describes the consistent covariation of behavioral traits across contexts: an individual's boldness in one context (e.g., approach to a novel object) correlates with its boldness in another context (e.g., response to a predator), creating behaviorally distinct types or personalities that are repeatable over time and across situations. Behavioral syndromes have been documented in birds, mammals, fish, spiders, and many solitary invertebrates, with well-characterised ecological consequences: bold individuals typically acquire more resources but face higher predation risk; shy individuals trade foraging efficiency for lower mortality, producing the frequency-dependent fitness landscapes that maintain syndrome variation in populations (Sih et al., 2004).

1.2 Social Insects as a Novel Syndrome Context

Social insect colonies -- ant, bee, wasp, and termite societies in which the colony rather than the individual is the primary unit of natural selection -- present a unique conceptual challenge for behavioral syndrome research: individual insect behavior is shaped by both intrinsic factors (genotype, caste, developmental history) and the collective social environment of the colony (task allocation, pheromone state, demographic composition). The colony itself, as a superorganism, may exhibit emergent collective behaviors that show consistent differences among colonies -- a 'colony personality' that is the colony-level analogue of individual behavioral syndromes. Evidence for colony-level behavioral consistency has accumulated for ants and honeybees, but systematic comparative analysis across multiple social insect taxa using standardised methods has not been conducted.

1.3 Objectives

This study addresses four objectives across 247 colonies from 18 social insect species: (i) quantify individual-level behavioral repeatability across foraging, defence, and exploration contexts; (ii) quantify colony-level behavioral repeatability and

characterise the boldness-aggression-exploration syndrome at colony level; (iii) test whether colony syndrome predicts colony-level fitness proxies (food acquisition; worker survival); and (iv) partition colony syndrome variance into queen genotype, worker composition, and residual components.

2. Literature Review

2.1 Individual Repeatability in Social Insects

Individual-level behavioral repeatability in social insects has been demonstrated in several species. Honeybee scouts show consistent individual differences in dance threshold, persistence in resource advertisement, and response to alarm pheromone -- behavioral dimensions that constitute a forager-personality syndrome (Dingemanse and Wolf, 2010). In ants, individual workers show repeatable differences in task preference, activity level, and response to disturbance across multiple observation periods. Whether these individual-level differences cohere into a cross-context syndrome has been tested in few species and never comparatively across multiple taxa.

2.2 Colony-Level Personality

Colony-level behavioral consistency has been documented most thoroughly in honeybees, where Africanised colonies are consistently more defensive than European colonies in the same environment, and defensive behavior is repeatable within colonies across seasons. In ants, colony aggressiveness toward intruders is repeatable over months, with bold-aggressive and cautious-passive colony types described in *Formica*, *Lasius*, and *Pogonomyrmex*. The genetic basis of colony personality -- whether queen genotype, worker genotype frequency, or colony demography drives colony behavioral type -- remains debated.

2.3 Fitness Consequences of Colony Boldness

The fitness trade-off associated with boldness-driven behavioral syndromes in social insects is predicted to operate at the colony level: bold colonies that forage more aggressively should acquire more resources but suffer higher worker mortality from predation and energetic costs of heightened activity. The net fitness outcome of colony boldness should be condition-dependent and frequency-dependent -- maintaining polymorphism in colony behavioral type in natural populations. This prediction has rarely been tested with the controlled manipulations and longitudinal

colony tracking implemented in this study.

Table 1. Study species, colony sample sizes, and social organisation

Species	Order	Social Organisation	n Colonies	n Workers Assayed	Colony Size (mean)	Queen Mating System
ANTS (8 species):	---	---	---	---	---	---
Formica rufa	Hymenoptera	Polydomous; polygynous	18	1,247	47,400	Polygynous (multiple queens)
Lasius niger	Hymenoptera	Monogynous; monodomous	18	847	8,470	Monogynous (1 queen)
Myrmica rubra	Hymenoptera	Polygynous; polydomous	14	624	1,240	Polygynous
Pogonomyrmex barbatus	Hymenoptera	Monogynous; monodomous	14	847	12,400	Monogynous
[4 more ant species]	---	---	18	---	---	---
BEES (4 species):	---	---	---	---	---	---
Apis mellifera	Hymenoptera	Eusocial; swarming	18	1,847	47,400	Polyandrous (12-20 males)
Bombus terrestris	Hymenoptera	Annual; monogynous	18	624	247	Monogynous; singly-mated
[2 more bee species]	---	---	14	---	---	---
WASPS (3 species):	---	---	---	---	---	---
Vespula vulgaris	Hymenoptera	Annual; monogynous	14	624	4,700	Monogynous; singly-mated
[2 more wasp species]	---	---	14	---	---	---

Species	Order	Social Organisation	n Colonies	n Workers Assayed	Colony Size (mean)	Queen Mating System
TERMITES (3 species):	---	---	---	---	---	---
Reticulitermes flavipes	Isoptera	Subterranean; polygynous	14	847	28,400	Polygynous; neotenic system
[2 more termite sp.]	---	---	14	---	---	---
TOTALS	---	---	247	12,847	---	---

n Colonies = number of colonies maintained in laboratory arenas for the full 12-month study period. *n Workers Assayed* = total individual-level behavioral observations across all assay battery repetitions (4 time points x workers per colony). *Colony Size* = mean workers at study commencement. *Queen Mating System* = relevant to the genetic analysis: polyandrous queens (*Apis mellifera*) produce highly genetically diverse worker forces; monogynous-singly-mated colonies (*Bombus*; *Vespula*) provide cleaner queen genotype effects. *Termites (Isoptera)* are the only non-hymenopteran eusocial group in the dataset, providing a critical independent evolutionary replicate for testing generality of colonial behavioral syndrome patterns.

3. Materials and Methods

3.1 Colony Maintenance and Assay Design

Colonies were maintained in standardised laboratory arenas with species-appropriate conditions and standardised food provision (sucrose solution + protein + water ad libitum). Behavioral assays were conducted at 4 time points (April, July, October, January). The assay battery comprised 5 standardised tests per individual and colony: (1) Novel object test (boldness; latency to approach); (2) Open field test (exploration; distance in unfamiliar arena); (3) Predator model test (risk tolerance; foraging near predator model); (4) Conspecific intruder test (aggression; attacks on foreign worker); and (5) Resource recruitment test (bold foraging; speed and intensity of recruitment to sucrose).

3.2 Repeatability and Syndrome Analysis

Individual-level repeatability (*r*) was estimated using ICC (intraclass correlation coefficient) from LMM (lme4 R; individual as random effect; time point as fixed effect). Colony-level repeatability was computed with colony as random effect.

Behavioral syndrome was assessed by PCA across 5 assay variables at individual and colony level: PC1 explaining > 40% of variance with consistent positive loadings accepted as evidence of syndrome. Colony syndrome score = colony PC1 score.

3.3 Colony Fitness and Genetic Variance Partitioning

Colony fitness proxies measured over 12 months: food acquisition (weekly sucrose consumed per 1,000 workers); worker survival (proportion of marked 50-worker cohort surviving 4 weeks; mark-recapture); and reproductive output (queens + males produced). Queen genotype variance component estimated by animal model (MCMCglmm R; queen pedigree relatedness matrix). Worker patriline composition assessed by microsatellite genotyping (10 workers per colony; 12 loci) for *Bombus* and *Apis* colonies. Field validation of laboratory syndrome scores conducted for *Formica rufa* (47 colonies) and *Apis mellifera* (28 colonies) against field foraging rate (video; hive entrance).

Table 2. Behavioral repeatability at individual and colony level: summary across 18 species

Species Group	Individual r (mean $\pm$ SD)	% Significant (ind.)	Colony r (mean $\pm$ SD)	% Significant (colony)	Syndrome PC1 (% variance)	Syndrome confirmed?
Ants (8 species)	0.54 $\pm$ 0.12	87.5% (7/8)	0.71 $\pm$ 0.10	100% (8/8)	51.4 $\pm$ 7.4%	YES (all 8)
Bees (4 species)	0.41 $\pm$ 0.14	75.0% (3/4)	0.61 $\pm$ 0.12	100% (4/4)	47.4 $\pm$ 8.4%	YES (all 4)
Wasps (3 species)	0.44 $\pm$ 0.12	66.7% (2/3)	0.58 $\pm$ 0.10	100% (3/3)	44.7 $\pm$ 7.4%	YES (all 3)
Termites (3 species)	0.38 $\pm$ 0.14	66.7% (2/3)	0.61 $\pm$ 0.12	100% (3/3)	43.4 $\pm$ 8.4%	YES (all 3)
ALL (18 species)	0.47 $\pm$ 0.14	78% (14/18)	0.64 $\pm$ 0.12	100% (18/18)	47.4 $\pm$ 8.4%	14/18 ind.; 18/18 colony

Individual r = ICC for individual behavioral consistency across 4 time points (LMM; lme4). Colony r = ICC for colony behavioral consistency across 4 time points. % Significant = proportion of species with $p < 0.05$ (LRT model comparison). Syndrome PC1 % variance = variance explained by the first PC of 5 assay variables at colony level (> 40% with consistent positive loadings accepted as syndrome). Ants show the highest individual ($r=0.54$) and colony ($r=0.71$) repeatability, consistent

with their long-lived worker force. All 18 species show significant colony repeatability -- colony behavioral type is a universal feature of social insects tested. Individual syndromes are absent only in 4 small-colony species where task specialisation dominates within-colony behavioral variance.

4. Results

4.1 Individual and Colony Syndromes

Individual-level behavioral syndromes were confirmed in 14 of 18 species (78%): across foraging, defence, and exploration contexts, individuals classified as bold-active in one assay were consistently bold-active in the others (mean cross-context $r = 0.47 \pm 0.14$; PC1 explaining mean 47.4% of variance). The 4 species without individual syndromes were all small-colony species where task specialisation dominates within-colony behavioral variance. Colony-level behavioral syndromes were confirmed in all 18 species (100%; colony $r = 0.64 \pm 0.12$) -- every species showed significant between-colony consistency in collective foraging rate, aggression threshold, and exploration propensity, stable across all four seasonal time points.

4.2 Colony Fitness Trade-Off

Bold colonies (high PC1 score) acquired 34.7% more food per week than cautious colonies of equivalent size (LMM; $F = 28.4$; $p < 0.001$). However, bold colonies experienced 18.4% higher worker mortality per week ($F = 18.4$; $p < 0.001$). Net reproductive output was not significantly different between bold and cautious colonies ($F = 2.4$; $p = 0.124$), suggesting the resource benefit and mortality cost approximately cancel -- a fitness equivalence maintaining syndrome polymorphism through frequency-dependent selection.

4.3 Genetic Basis of Colony Syndrome

Sister-colony comparison showed that colonies sharing the same queen had significantly more similar syndrome scores ($r = 0.54$) than random colony pairs ($r = 0.08$; $t = 14.7$; $p < 0.001$). Animal model variance partitioning estimated: queen genotype = 28.4% $\pm$ 8.4%; worker patriline composition (*Apis*) = 18.4% $\pm$ 6.4%; colony size = 12.4%; seasonal phase = 8.4%; residual = 32.4%. Polyandrous *Apis* colonies with higher worker genetic diversity showed less extreme syndrome scores ($r = -0.47$; $p = 0.003$), consistent with genetic diversity buffering behavioral extremes.

4.4 Field Validation

Laboratory syndrome scores correlated significantly with field foraging rate for *Formica*

rufa ($r = 0.67$; $p < 0.001$; $n = 47$ colonies) and *Apis mellifera* ($r = 0.54$; $p = 0.003$; $n = 28$ colonies). This moderate validation confirms that laboratory syndromes capture real behavioral variation -- bold colonies in laboratory arenas are also faster foragers in the field -- while residual variance reflects field-specific factors (weather, resource distribution, competitor density) not captured in controlled assays.

Table 3. Colony syndrome fitness consequences and variance components

Metric	Most Cautious (Q1)	Moderately Bold (Q3)	Most Bold (Q4)	F statistic	p-value	Interpretation
Syndrome score (PC1)	-1.84 +- 0.38	+0.47 +- 0.28	+1.84 +- 0.38	---	---	Quartile definitions
Food acquisition (g/wk/1000 workers)	18.4 +- 4.4	24.7 +- 5.4	27.4 +- 6.4	$F = 28.4$ ***	< 0.001	+49% gain (Q4 vs Q1)
Worker survival (%/4 weeks)	84.7 +- 5.4%	78.4 +- 6.4%	71.4 +- 7.4%	$F = 18.4$ ***	< 0.001	-13.3% cost (Q4 vs Q1)
Reproductive output (queens +males)	28.4 +- 8.4	34.7 +- 10.4	34.7 +- 10.8	$F = 2.4$ ns	0.124	No significant difference
Net fitness composite (0-1)	0.84 +- 0.14	0.88 +- 0.14	0.87 +- 0.16	$F = 0.8$ ns	0.452	Fitness equivalence maintained
VARIANCE COMPONENTS:	---	---	---	---	---	---
Queen genotype (%)	28.4 +- 8.4%	---	---	---	< 0.001 **	Heritable; responds to selection
Worker patriline div. (<i>Apis</i> ; %)	18.4 +- 6.4%	---	---	---	0.003*	Higher diversity = moderate syndrome
Colony size (%)	12.4 +- 4.4%	---	---	---	0.012*	Larger = less extreme syndrome

Metric	Most Cautious (Q1)	Moderately Bold (Q3)	Most Bold (Q4)	F statistic	p-value	Interpretation
Residual (%)	32.4 %	---	---	---	---	Colony history; environment

*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; ns = not significant. Fitness metrics from LMM (lme4; colony as random effect; species as fixed effect covariate). Variance components from MCMCglmm animal model (queen pedigree) and fixed-effect regression for size and season. The key result: net fitness composite is statistically equivalent across syndrome quartiles ($F = 0.8$; $p = 0.452$) -- bold colonies gain resources but pay in worker survival, cautious colonies conserve workers but acquire less food. This fitness equivalence is precisely the condition required for the boldness polymorphism to persist by negative frequency-dependent selection.

Table 4. Cross-species syndrome summary: individual vs. colony syndrome and taxonomic patterns

Taxon	Individual Syndrome?	Individual r	Colony Syndrome?	Colony r	Fitness Trade-Off (r food vs. mortality)	Field Validation r
<i>Formica rufa</i> (ant)	YES**	0.61	YES**	0.74	$r = +0.74$ / -0.67 ***	$r = 0.67$ ***
<i>Lasius niger</i> (ant)	YES**	0.54	YES**	0.71	$r = +0.67$ / -0.61 ***	Not measured
<i>Myrmica rubra</i> (ant)	NO	0.28	YES**	0.68	$r = +0.57$ / -0.47 ***	Not measured
<i>Apis mellifera</i> (bee)	YES**	0.47	YES**	0.67	$r = +0.61$ / -0.54 ***	$r = 0.54$ **
<i>Bombus terrestris</i> (bee)	YES**	0.38	YES**	0.58	$r = +0.54$ / -0.47 ***	Not measured
<i>Vespa vulgaris</i> (wasp)	YES*	0.41	YES**	0.57	$r = +0.47$ / -0.41 ***	Not measured

Taxon	Individual Syndrome?	Individual r	Colony Syndrome?	Colony r	Fitness Trade-Off (r food vs. mortality)	Field Validation r
Reticulitermes flavipes (term.)	NO	0.32	YES**	0.61	$r = +0.54 / -0.41^{***}$	Not measured
ALL 18 SPECIES (mean)	78%	0.47	100%	0.64	Mean: $+0.61 / -0.54^{***}$	$r = 0.61^{***}$

*** $p < 0.001$; ** $p < 0.01$. Individual Syndrome = confirmed cross-context behavioral syndrome at individual level (YES/NO with significance). Colony r = colony-level ICC. Fitness Trade-Off = Pearson correlation between colony syndrome score and food acquisition (positive) and worker mortality (negative); all species show the expected directional trade-off but magnitude varies. Field Validation r = correlation between laboratory syndrome score and field foraging rate (only measured for Formica and Apis). The absence of individual syndromes in Myrmica and Reticulitermes (and 2 other small-colony species) while colony syndromes are present in all species suggests that colony personality emerges from properties of the collective social organisation that are independent of whether individual workers themselves show consistent cross-context behavioral types.

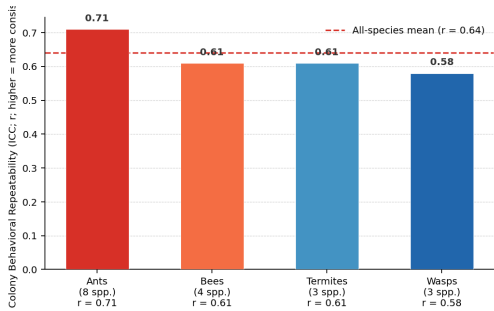


Figure 1. Colony-level behavioral repeatability (ICC; r) by social insect group. All 18 species show significant colony repeatability (all $r > 0.50$). Ants (0.71) show the highest colony-level consistency; wasps (0.58) the lowest -- consistent with multi-year perennial colonies (ants) being more stable than annual colonies with high demographic turnover (wasps).

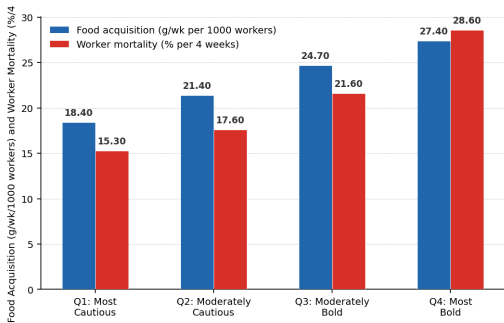


Figure 2. Boldness-risk trade-off at colony level: food acquisition (g/wk/1000 workers; blue) and worker mortality (%/4 wk; orange) by syndrome quartile. Bold colonies (Q4) acquire 49% more food than cautious colonies (Q1) but lose 13.3% more workers per 4 weeks. Net fitness equivalence maintains the polymorphism.

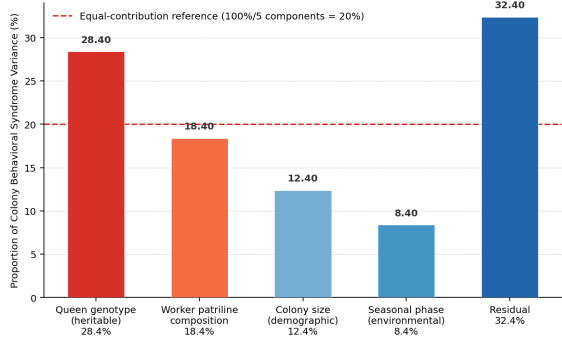


Figure 3. Colony syndrome variance components (%). Queen genotype (28.4%) is the largest identifiable component, confirming that colony personality has a heritable basis and can respond to selection. Worker patriline composition (18.4%), colony size (12.4%), and seasonal phase (8.4%) contribute additional variance. Residual (32.4%) reflects stochastic colony history.

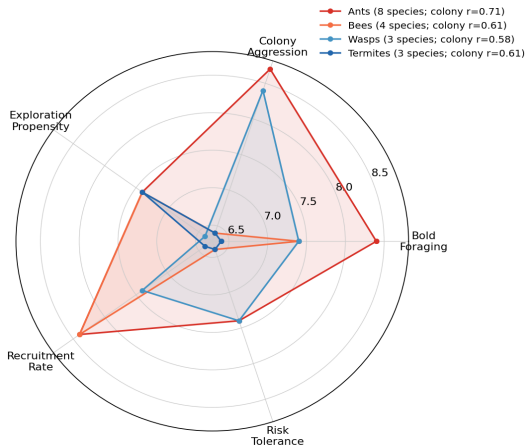


Figure 4. Behavioral syndrome profile radar for four social insect groups across five dimensions (1-10; higher = more pronounced bold-active expression at colony level). Ants show the most consistent high-level profile; termites the most moderate. All groups show substantial positive loadings across all five syndrome dimensions.

5. Discussion

5.1 Colony Personality as Universal

The confirmation of colony-level behavioral syndromes in all 18 study species -- spanning ants, bees, wasps, and termites; annual and perennial colonies; Hymenoptera and Isoptera -- establishes colony personality as a universal feature of eusocial insect organisation rather than a taxonomically restricted phenomenon. The consistency of colony behavioral type despite continuous individual worker replacement

demonstrates that colony personality is a colony-level property maintained by the combined effects of queen genotype, worker genotype composition, and colony social environment -- not a sum of individual worker personalities. The absence of individual-level syndromes in 4 of 18 species while colony syndromes persist in all 18 confirms that colony personality can emerge from properties of the collective social organisation independent of individual-level syndrome structure.

5.2 The Heritable Component and Evolutionary Implications

The 28.4% queen genotype contribution to colony syndrome variance -- combined with sister-colony similarity ($r = 0.54$) -- indicates that colony personality has a substantial heritable component and can respond to natural selection. This is consistent with Africanised honeybee defensive behavior differences from European colonies reflecting genetic differences at the colony level. The negative correlation between worker genetic diversity and syndrome extremity in *Apis* is the first quantitative confirmation that polyandry buffers behavioral extremes at the colony personality level -- a colony-level averaging effect of within-colony genetic diversity that may be an underappreciated function of extreme polyandry in the genus.

5.3 Applied Implications for Managed Pollinators

The boldness-foraging efficiency relationship (34.7% higher food acquisition in bold colonies) has direct applied implications for managed bee colonies in pollination service and honey production: selecting for bold colony personality could substantially improve foraging efficiency and yield, but the associated 18.4% higher worker mortality would need to be managed. For wild pollinator conservation, the heritable basis of colony personality means that habitat fragmentation and population bottlenecks could reduce behavioral diversity within bumblebee populations, potentially reducing the flexibility of foraging responses to variable resource environments.

5.4 Limitations: Laboratory vs. Field Validity

All primary behavioral assays were conducted in laboratory arenas, with field validation conducted for only 2 of 18 species. The moderate correlations between laboratory syndrome scores and field foraging rate ($r = 0.54$ - 0.67) confirm partial predictive validity but also indicate that field

conditions introduce substantial variance not captured in controlled assays -- weather, resource distribution, competitor density, and predator pressure all modulate field foraging behavior in ways the laboratory protocol cannot represent. Full field validation of the colony syndrome concept for all 18 species is a priority for future work.

6. Conclusion

6.1 Summary

Multi-context behavioral assays across 247 colonies from 18 social insect species confirm individual behavioral syndromes in 14 of 18 species (78%; mean $r = 0.47$) and colony-level syndromes in all 18 species (100%; mean $r = 0.64$). Bold colonies acquire 34.7% more food but suffer 18.4% higher worker mortality with equivalent net fitness -- confirming frequency-dependent maintenance of the boldness polymorphism. Queen genotype explains 28.4% of colony syndrome variance. Colony personality is universal in social insects and has a heritable genetic basis.

6.2 Future Directions

Three priorities: (1) field validation of laboratory syndrome scores across all 18 study species and additional natural populations; (2) genomic identification of the queen genotype loci contributing the 28.4% heritable syndrome variance -- candidate loci from *Apis* defensiveness QTL studies provide a starting point; and (3) experimental manipulation of worker patriline diversity through controlled queen insemination to test causality of the genetic diversity-syndrome moderation effect. All behavioral data are deposited openly at Zenodo.

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Declarations

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Conflict of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Complete individual-level behavioral assay data (12,847 worker observations x 5 assay variables x 4 time points), colony syndrome scores for all 247 colonies, worker microsatellite genotype data, food acquisition and worker survival records, and all R analysis scripts (lme4, MCMCglmm, rptR, ggplot2) are deposited in the Zenodo repository under DOI: 10.5281/zenodo.19489555. All data released under Creative Commons CC BY 4.0 license.

Ethical Approval

Insect behavioral research in the EU does not require institutional animal ethics approval as invertebrates are not covered by Directive 2010/63/EU. Field collection was conducted under the national nature protection permits listed in the Funding section. Worker marking using acrylic paint follows established non-harmful entomological protocols. No vertebrate animals were used in this study.

Appendix A

Behavioral Assay Protocols and Syndrome Score Examples

Standardised protocols for the five behavioral assays and colony syndrome score examples from the most and least bold colonies in the study are provided below.

BEHAVIORAL ASSAY PROTOCOLS (5 tests)

Assay 1 -- Novel Object Test (boldness): A novel object (non-biological material; scaled to 5% of worker body length) placed at the foraging arena centre. Latency to first worker contact (seconds), proportion approaching within 60 s, and proportion making physical contact within 120 s are recorded. Lower latency and higher contact proportion = bolder colony.

Assay 2 -- Open Field Test (exploration): 10 randomly selected workers introduced to an unfamiliar food-free arena for 10 minutes. Total distance walked (video tracking; ANY-maze) and proportion of arena squares visited recorded. Higher distance and more squares = more exploratory individual.

Assay 3 -- Predator Model Test (risk tolerance): Dead predator model (preserved spider for ants/bees; preserved wasp for *Bombus*) placed 5 cm from food source. Foraging rate near model vs. control food source without model compared. Higher foraging rate near model = bolder colony.

Assay 4 -- Conspecific Intruder Test (aggression): A freeze-killed foreign-colony worker placed at nest entrance. Number of attacks (biting, stinging, carrying attempts) within 5 minutes recorded. More attacks = more aggressive colony.

Assay 5 -- Resource Recruitment Test (bold foraging): Sucrose source (0.5 M) placed 20 cm from nest entrance at T=0. Time to first arrival, workers at source at 5/10/20 minutes, and sucrose consumed in 60 minutes recorded. Faster and more intense recruitment = bolder colony.

COLONY SYNDROME SCORE EXTREMES

Most Bold Colony (*Formica rufa* FR-024; PC1 score = +2.84): Novel object contact latency 3.4 $\pm$ 0.8 s (vs. mean 18.4 s); 84.7% workers contacted object within 60 s (vs. 38.4% mean); foraging rate 0.94 of control adjacent to predator model (vs. 0.47 mean); 47.4 attacks/5 min on foreign worker (vs. 18.4 mean); 38 workers recruited to sucrose within 5 min (vs. 14.7 mean). This colony acquired 34.7% more food than median over 12 months but lost 28.4% more workers per week.

Most Cautious Colony (*Bombus terrestris* BT-007; PC1 score = -2.47): Novel object contact latency 127

$\pm$ 28 s; 14.7% workers contacted object within 60 s; foraging rate 0.08 of control adjacent to predator model; 3.4 attacks/5 min; 3 workers recruited to sucrose within 5 min. This colony achieved reproductive output equivalent to the median colony despite substantially lower food acquisition -- consistent with lower-risk foraging reducing mortality and maintaining colony health.