



The behavioral ecology of variation in social insects

JM Jandt^{1,3} and DM Gordon²

Understanding the ecological relevance of variation within and between colonies has been an important and recurring theme in social insect research. Recent research addresses the genomic and physiological factors and fitness effects associated with behavioral variation, within and among colonies, in regulation of activity, cognitive abilities, and aggression. Behavioral variation among colonies has consequences for survival and reproductive success that are the basis for evolutionary change.

Addresses

¹Iowa State University, Department of Ecology, Evolution, and Organismal Biology, 251 Bessey Hall, Ames, IA 50011, USA

²Stanford University, Department of Biology, Gilbert Biological Sciences Building, rm 410, 371 Serra Mall, Stanford, CA 94305, USA

Corresponding author: Jandt, JM (jjandt2@gmail.com)

³Present address: Otago University, Department of Zoology, 340 Great King Street, Dunedin 9016, New Zealand.

Current Opinion in Insect Science 2016, 15:40–44

This review comes from a themed issue on **Behavioural ecology**

Edited by **Lars Chittka** and **Deborah M Gordon**

For a complete overview see the [Issue](#) and the [Editorial](#)

Available online 2nd March 2016

<http://dx.doi.org/10.1016/j.cois.2016.02.012>

2214-5745/© 2016 Elsevier Inc. All rights reserved.

Introduction

Investigating the sources of variation has been an important and recurring theme in social insect research [1]. Here we consider variation at two levels: among individuals within colonies, and among colonies within populations. Because of space limitations we do not provide a comprehensive review; each of our citations is only one example out of many studies.

Variation among individuals within colonies is ubiquitous. In addition, evidence is growing that colonies vary, which means that the range of individual phenotypes in one colony differs from the range in another. The behavior of colony A differs from the behavior of colony B because the combined outcome of the range of behavior among individuals of colony A differs from that combined outcome for colony B.

Many kinds of phenotypic differences lead to both individual and colony variation (reviewed in [2–4]); including: life-history traits (i.e., growth, reproduction, and queen

mating frequency [5–10]), morphological traits related to social behavior and physiology [11*,12,13,14*,15,16,17,18], and behavioral traits (i.e., regulation of activity, cognitive abilities, or aggression and nestmate recognition [19*,20,21]). The development and maintenance of individual and colony variation is influenced by resource availability, abiotic conditions along a geographic cline, social interactions within and between colonies, and population-level genetic factors such as dependent lineages (reviewed in [22]). In most cases, we do not know the source of variation among individuals or colonies. Mutation, small differences in microclimate and resource availability, the developmental noise that leads organisms with the same genotypes to differ, all probably contribute to the variation that we observe.

Behavioral variation

Regulation of activity

Individuals within a colony may exhibit consistent behavioral variation (see Table 2 in [3]) in their propensity to perform particular tasks [19*]. Whether individuals work inside or outside the nest may be associated with a tendency to be in a certain location inside the nest, which affects the probability of interaction with nestmates [23,24]. In the ant *Myrmica rubra*, individuals that forage outside the nest are more active, exploratory, aggressive, and attracted to light than individuals that work inside nest [25]. Individuals often move from one task to another as they age, for example, from in-nest brood care to nest cleaning to out-of-nest foraging. The mechanisms for this have been best studied in honey bees (reviewed in [26]). In the ant *Camponotus fellah*, the age-mediated transition from in-nest to foraging tasks also corresponds to changes in social interaction networks [23]. Individuals within a colony may also vary in foraging strategies. In *Ectatomma ruidum*, some foragers are more likely to collect food by stealing from neighboring nests while others are more likely to collect food by searching the leaf-litter [27,28]. Colony variation in foraging behavior may then arise from variation in the foraging strategies of individuals.

Studies on behavioral variation among colonies have focused on the regulation of activity [29,30,31,32*,33]; for example, foraging behavior [34], thermoregulation, and nest cleaning [35*]. Harvester ant colonies differ consistently, from year to year, in the extent to which they curtail foraging activity in dry conditions. Because individual ants live only a year (whereas the queen lives for 20–30 years, and does not begin producing new reproductives until she is five [36]), consistent differences are apparently inherited in successive cohorts of workers

[37]. Since the regulation of foraging depends on interactions between outgoing and returning foragers [38,39], it is likely that differences among colonies arise from the variation in individual sensitivity to interactions.

Colonies of bumble bees [40] and honey bees [41] vary in the extent of nectar and pollen foraging. In honey bees, genomic and physiological differences are associated with consistent within-colony variation in individual foraging behavior [26,42]. Social insect colonies also vary in their ability to thermoregulate and clean the nest [35^{*}], probably due to physiological variation among individuals within the colony in ability to perceive temperature fluctuations [43,44] or dead nestmates and parasites [35^{*},45,46].

Cognitive abilities

Individuals and colonies vary in learning, memory, sensory bias, and decision-making [3]. In bumble bees, rapid learning is correlated with the ability to remember visual cues [47], and rate of decision-making is associated with nectar foraging [20]. Colonies that learn more slowly harvest less nectar compared to the fastest learning colonies [48]. Colonies also vary in sensory bias, such as color preferences, which may be associated with variation in foraging success and exploratory behavior [49]. For example, colonies of bumble bees that prefer violet collect more nectar than those that prefer blue [20].

Aggression and nestmate recognition

Individuals and colonies may both vary in aggression toward individuals of other colonies [3]. Differences among colonies in cuticular hydrocarbon (CHC) profile are the basis for nestmate recognition in most social insects. The results of nestmate recognition experiments in ants suggest that individuals modify over time their response to the odors of different ants that they meet, so that at any time individuals differ in their responses. Collectively, colonies respond because there are some ants that can identify the odor of any intruder as that of a non-nestmate [21]. Empirical studies suggest that environmental factors might predict CHC profile better than colony of origin [50–52]. For example, leaf-cutter ant colonies (*Atta sextens*) that forage on the same plants have similar CHC profiles and are less aggressive toward one another than toward conspecifics with a different diet [53].

In some *Polistes* spp. (Vespidae, Polistinae), individuals assess variation among workers by their facial patterns. In *P. dominula*, specific facial patterns, such as the distribution of the black pigment on the clypeus, are associated with dominance rank and nesting success [54]. In *P. fuscatus*, workers can distinguish individual faces of both nestmates and non-nestmates [55]. In the hover wasp, *Liozenogaster flavolineata* (Vespidae, Stenogastrinae),

individuals prioritize visual facial cues over CHC profiles to distinguish nestmates [56].

An individual's age or size may be associated with aggression or exploratory behavior. For example, aggression in the wasp, *Vespula vulgaris*, tends to increase with age [57]. In the ant *Leptothorax acervorum*, older workers with well-developed ovaries tend to be more aggressive and active than younger ones [58^{*}]. In some ant species, larger or major workers tend to be more aggressive than smaller workers (e.g., *Acromyrmex echinator*, [59]; *Oecophylla smaragdina*, [60]).

Aggressive behavior appears to be heritable (reviewed for honey bees in [26]), but changes in gene expression are also associated with variation in aggressive behavior. In weaver ants, high expression of octopamine is linked to aggressive behavior [60], whereas in honey bees, octopamine, as well as glutamate and GABA signaling, is linked to exploratory behavior [61,62^{**}]. Aggression in honey bees, as in *Polistes metricus* paper wasps, is linked to a decrease in oxidative phosphorylation [63–65].

Ecological sources and outcomes of variation

Environmental conditions lead to variation among colonies in life history traits within a species across a geographic cline. For example, a temperature gradient is associated with variation in colony growth and activity in subterranean termites [66,67]. Gradients in environmental conditions are associated with intraspecific variation among colonies in life-history and breeding structure [68–70], in resource use [30], and in interactions with other colonies [71] or other species such as pathogens [72–74] and parasitoids [75].

Variation among colonies in behavior can have important ecological effects. For example, differences among harvester ant colonies in the regulation of foraging by feedback from ant–ant interactions [29,76], are associated with differences in reproductive success, in numbers of offspring colonies [37,77]. This suggests that selection is acting on variation among colonies in how individuals respond to interactions. Colony variation in interaction networks can lead to differences in parasite load and susceptibility to infection [78,79].

Variation among colonies may facilitate rapid evolution of invasive species [80,81]. Aggressive and active colonies may have a competitive advantage in the invasive range [82,83], until population densities become very high [81]. When the invasive wasp *Vespa velutina* is sympatric with the native wasp *Vespa crabro*, its foundresses tend to be more active, bolder, and more exploratory than the native species [84^{*}]. On the other hand, there is more variation in these traits among the native *V. crabro* foundresses, perhaps because of a genetic bottleneck effect on *V. velutina* when they were introduced

[84*]. In the fire ant (*Solenopsis invicta*), colonies vary in queen number, due to epigenetic processes involving large numbers of genes [85]. A polygynous form spread within the invasive range [86] that may be associated with a decrease in aggression and high population densities [87].

Conclusions

Investigating the sources of variation is a central question in evolutionary biology. Variation is a fundamental element of the phenotypes that matter ecologically, and it is the starting point for evolutionary change. Variation among individuals, and among colonies, arises from differences in their behavioral, physiological and epigenetic response to their environments. Environments change, sometimes because organisms modify them, and this amplifies variation. It seems likely that when we compare individuals and colonies in any aspect of their biology, we will find that they vary.

Acknowledgement

JM Jandt acknowledges funding provided by NSF: IOS-1146410.

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
 - of outstanding interest
1. Jeanne RL: *Interindividual Behavioral Variability in Social Insects*. Westview Press; 1988.
 2. LeBoeuf AC, Grozinger CM: **Me and we: the interplay between individual and group behavioral variation in social collectives**. *Curr Opin Insect Sci* 2014, **5**:16-24.
 3. Jandt JM, Bengston S, Pinter-Wollman N, Pruitt JN, Raine NE, Dornhaus A, Sih A: **Behavioural syndromes and social insects: personality at multiple levels**. *Biol Rev* 2014, **89**:48-67.
 4. Jeanson R, Weidenmuller A: **Interindividual variability in social insects – proximate causes and ultimate consequences**. *Biol Rev* 2014, **89**:671-687.
 5. Marti HE, Carlson AL, Brown BV, Mueller UG: **Foundress queen mortality and early colony growth of the leafcutter ant, *Atta texana* (Formicidae, Hymenoptera)**. *Insect Soc* 2015, **62**:357-363.
 6. Miyazaki S, Yoshimura M, Saiki R, Hayashi Y, Kitade O, Tsuji K, Maekawa K: **Intracolony genetic variation affects reproductive skew and colony productivity during colony foundation in a parthenogenetic termite**. *BMC Evol Biol* 2014, **14**:177.
 7. Wills BD, Moreau CS, Wray BD, Hoffmann BD, Suarez AV: **Body size variation and caste ratios in geographically distinct populations of the invasive big-headed ant, *Pheidole megacephala* (Hymenoptera: Formicidae)**. *Biol J Linn Soc* 2014, **113**:423-428.
 8. Kramer BH, Schrempf A, Scheuerlein A, Heinze J: **Ant colonies do not trade-off reproduction against maintenance**. *PLOS ONE* 2015, **10**:e0137969.
 9. Loope KJ, Chien C, Juhl M: **Colony size is linked to paternity frequency and paternity skew in yellowjacket wasps and hornets**. *BMC Evol Biol* 2014, **14**:277.
 10. Heinze J, Gratiashvili N: **High skew in the Caucasus: functional monogyny in the ant *Leptothorax samni***. *Insect Soc* 2015, **62**:385-392.
 11. Alvarado S, Rajakumar R, Abouheif E, Szyf M: **Epigenetic variation in the *Egfr* gene generates quantitative variation in a complex trait in ants**. *Nat Commun* 2015, **6**.
The production of continuous size variation of *Camponotus* ant workers is regulated via DNA methylation, specifically through the conserved cell-signalling gene *Epidermal growth factor receptor*.
 12. Rajakumar R, San Mauro D, Dijkstra MB, Huang MH, Wheeler DE, Hiou-Tim F, Khila A, Cournoyea M, Abouheif E: **Ancestral developmental potential facilitates parallel evolution in ants**. *Science* 2012, **335**:79-82.
 13. Grüter C, Menezes C, Imperatriz-Fonseca VL, Ratnieks FLW: **A morphologically specialized soldier caste improves colony defense in a neotropical eusocial bee**. *Proc Natl Acad Sci U S A* 2012, **109**:1182-1186.
 14. Segers FHID, Menezes C, Vollet-Neto A, Lambert D, Grüter C: **Soldier production in a stingless bee depends on rearing location and nurse behaviour**. *Behav Ecol Sociobiol* 2015, **69**:613-623.
The production of large workers in a stingless bee depends on the spatial arrangement of brood inside the nest. Larvae reared in the center of the nest grow in larger cells and are provisioned with more food than those raised elsewhere. Larger bees are more likely to guard the nest than smaller ones.
 15. del Castillo RC, Sanabria-Urbán S, Serrano-Meneses MA: **Trade-offs in the evolution of bumblebee colony and body size: a comparative analysis**. *Ecol Evol* 2015, **5**:3914-3926.
 16. Westling JN, Harrington K, Bengston S, Dornhaus A: **Morphological differences between extranidal and intranidal workers in the ant *Temnothorax rugatulus*, but no effect of body size on foraging distance**. *Insect Soc* 2014, **61**:367-369.
 17. Baudier KM, Mudd AE, Erickson SC, O'Donnell S: **Microhabitat and body size effects on heat tolerance: implications for responses to climate change (army ants: Formicidae, Ecitoninae)**. *J Anim Ecol* 2015, **84**:1322-1330.
 18. Couvillon MJ, Dornhaus A: **Small worker bumble bees (*Bombus impatiens*) are harder against starvation than their larger sisters**. *Insect Soc* 2010, **57**:193-197.
 19. Gordon DM: **From division of labor to collective behavior**.
• *Behav Ecol Sociobiol* 2015:1-8.
Variation among workers within colonies arises from the interplay of worker interactions with each other and their environments. This leads to ecologically important variation among colonies.
 20. Raine NE, Chittka L: **The adaptive significance of sensory bias in a foraging context: floral colour preferences in the bumblebee *Bombus terrestris***. *PLoS ONE* 2007, **2**.
 21. Esponda F, Gordon DM: **Distributed nestmate recognition in ants**. *Proc R Soc B – Biol Sci* 2015, **282**:20142838.
 22. Bengston SE, Jandt JM: **The development of collective personality: the ontogenetic drivers of behavioral variation across groups**. *Front Ecol Evol* 2014, **2**:81.
 23. Mersch DP, Crespi A, Keller L: **Tracking individuals shows spatial fidelity is a key regulator of ant social organization**. *Science* 2013, **340**:1090-1093.
 24. Pinter-Wollman N: **Persistent variation in spatial behavior affects the structure and function of interaction networks**. *Curr Zool* 2015, **61**:98-106.
 25. Pamminger T, Foitzik S, Kaufmann KC, Schutzler N, Menzel F: **Worker personality and its association with spatially structured division of labor**. *PLOS ONE* 2014, **9**:e79616.
 26. Dolezal A, Toth A: **Honey bee sociogenomics: a genome-scale perspective on bee social behavior and health**. *Apidologie* 2014, **45**:375-395.
 27. Jandt JM, Hunt EM, McGlynn TP: **Intraspecific food-robbing and neighborhood competition: consequences for anti-robbler vigilance and colony productivity**. *Biotropica* 2015, **47**:491-496.
 28. McGlynn TP, Graham R, Wilson J, Emerson J, Jandt JM, Jahren AH: **Distinct types of foragers in the ant *Ectatomma ruidum*: typical foragers and furtive thieves**. *Anim Behav* 2015, **109**:243-247.

29. Gordon DM, Guetz A, Greene MJ, Holmes S: **Colony variation in the collective regulation of foraging by harvester ants.** *Behav Ecol* 2011, **22**:429-435.
30. Kleeberg I, Jongepier E, Job S, Foitzik S: **Geographic variation in social parasite pressure predicts intraspecific but not interspecific aggressive responses in hosts of a slavemaking ant.** *Ethology* 2015, **121**:694-702.
31. Wray MK, Mattila HR, Seeley TD: **Collective personalities in honeybee colonies are linked to colony fitness.** *Anim Behav* 2011, **81**:559-568.
32. Bockoven AA, Wilder SM, Eubanks MD: **Intraspecific variation among social insect colonies: persistent regional and colony-level differences in fire ant foraging behavior.** *PLOS ONE* 2015, **10**:e0133868.
- Fire ant colonies vary in foraging activity, exploration, and discovery of and recruitment to resources. Variation in activity was correlated with colony growth, and there was evidence to suggest that activity and exploration are partially heritable.
33. Pinter-Wollman N, Gordon DM, Holmes S: **Nest site and weather affect the personality of harvester ant colonies.** *Behav Ecol* 2012, **23**:1022-1029.
34. Johnson BR, Frost E: **Individual-level patterns of division of labor in honeybees highlight flexibility in colony-level developmental mechanisms.** *Behav Ecol Sociobiol* 2012, **66**:923-930.
35. Jandt JM, Dornhaus A: **Bumblebee response thresholds and body size: does worker diversity increase colony performance?** *Anim Behav* 2014, **87**:97-106.
- Continuous variation in worker size and in fanning in response to temperature increase was measured in bumble bee colonies. Colonies varied in their overall performance of removing dead nestmates and cooling the nest. Colony corpse removal was correlated with the average body size of workers in the nest, whereas colony cooling was correlated with the amount of behavioral variation in the nest.
36. Gordon DM: **The development of organization in an ant colony.** *Am Sci* 1995, **83**:50-57.
37. Gordon DM: **The rewards of restraint in the collective regulation of foraging by harvester ant colonies.** *Nature* 2013, **498**:91-93.
38. Pless E, Queirolo J, Pinter-Wollman N, Crow S, Allen K, Mathur MB, Gordon DM: **Interactions increase forager availability and activity in harvester ants.** *PLOS ONE* 2015, **10**:e0141971.
39. Pinter-Wollman N, Bala A, Merrell A, Queirolo J, Stumpe MC, Holmes S, Gordon DM: **Harvester ants use interactions to regulate forager activation and availability.** *Anim Behav* 2013, **86**:197-207.
40. Saifuddin M, Jha S: **Colony-level variation in pollen collection and foraging preferences among wild-caught bumble bees (Hymenoptera: Apidae).** *Environ Entomol* 2014, **43**:393-401.
41. Oliveira-Abreu C, Hilario SD, Luz CFP, Ales-dos-Santos I: **Pollen and nectar foraging by *Melipona quadrifasciata anthidioides* Lepelletier (Hymenoptera: Apidae: Meliponini) in natural habitat.** *Sociobiology* 2014, **61**:441-448.
42. Page RE, Rueppell O, Amdam GV: **Genetics of reproduction and regulation of honeybee (*Apis mellifera* L.) social behavior.** *Annu Rev Genet* 2012, **46**:97-119.
43. Junca P, Sandoz J-C: **Heat perception and aversive learning in honey bees: putative involvement of the thermal/chemical sensor AmHsTRPA.** *Front Physiol* 2015, **6**:316.
44. Ramirez-Esquivel F, Zeil J, Narendra A: **The antennal sensory array of the nocturnal bull ant *Myrmecia pyriformis*.** *Arthropod Struct Dev* 2014, **43**:543-558.
45. Diez L, Moquet L, Detrain C: **Post-mortem changes in chemical profile and their influence on corpse removal in ants.** *J Chem Ecol* 2013, **39**:1424-1432.
46. Rocha FH, Lachaud J-P, Valle-Mora J: **Fine individual specialization and elitism among workers of the ant *Ectatomma tuberculatum* for a highly specific task: intruder removal.** *Ethology* 2014, **120**:1-14.
47. Raine NE, Chittka L: **No trade-off between learning speed and associative flexibility in bumblebees: a reversal learning test with multiple colonies.** *PLoS ONE* 2012, **7**:e45096.
48. Raine NE, Chittka L: **The correlation of learning speed and natural foraging success in bumble-bees.** *Proc R Soc B – Biol Sci* 2008, **275**:803-808.
49. Muller H, Grossmann H, Chittka L: **'Personality' in bumblebees: individual consistency in responses to novel colours?** *Anim Behav* 2010, **80**:1065-1074.
50. Sturgis SJ, Gordon DM: **Aggression is task dependent in the red harvester ant (*Pogonomyrmex barbatus*).** *Behav Ecol* 2013, **24**:532-539.
51. Liang D, Silverman J: **"You are what you eat": diet modifies cuticular hydrocarbons and nestmate recognition in the Argentine ant, *Linepithema humile*.** *Naturwissenschaften* 2000, **87**:412-416.
52. Khidr SK, Linforth RS, Hardy IC: **Genetic and environmental influences on the cuticular hydrocarbon profiles of *Goniozus wasps*.** *Entomologia Experimentalis et Applicata* 2013, **147**:175-185.
53. Valadares L, Nascimento D, Nascimento FS: **Foliar substrate affects cuticular hydrocarbon profiles and intraspecific aggression in the leafcutter ant *Atta sexdens*.** *Insects* 2015, **6**:141-151.
54. Tibbetts EA, Forrest T, Vernier C, Jinn J, Madagame A: **Socially selected ornaments and fitness: signals of fighting ability in paper wasps are positively associated with survival, reproductive success, and rank.** *Evolution* 2015, **69**:2917-2926.
55. Injaian A, Tibbetts EA: **Cognition across castes: individual recognition in worker *Polistes fuscatus* wasps.** *Anim Behav* 2014, **87**:91-96.
56. Baracchi D, Petrocelli I, Chittka L, Ricciardi G, Turillazzi S: **Speed and accuracy in nest-mate recognition: a hover wasp prioritizes face recognition over colony odour cues to minimize intrusion by outsider.** *Proc R Soc B* 2015, **282**:20142750.
57. Santoro D, Hartley S, Suckling DM, Lester PJ: **The stinging response of the common wasp (*Vespa vulgaris*): plasticity and variation in individual aggressiveness.** *Insect Soc* 2015, **62**:455-463.
58. Kühbandner S, Modlmeier AP, Foitzik S: **Age and ovarian development are related to worker personality and task allocation in the *Leptothorax acervorum*.** *Curr Zool* 2014, **60**:392-400.
- Worker behavior, including brood care, aggression, and exploration, was consistent within and across settings. Some workers had a more aggressive and exploratory personality type than others. Ovarian development and age were also associated with worker behavior.
59. Larsen J, Fouks B, Bos N, d'Ettorre P, Nehring V: **Variation in nestmate recognition ability among polymorphic leaf-cutting ant workers.** *J Insect Physiol* 2014, **70**:59-66.
60. Kamhi JF, Nunn K, Robson SKA, Traniello JFA: **Polymorphism and division of labour in a socially complex ant: neuromodulation of aggression in the Australian weaver ant, *Oecophylla smaragdina*.** *Proc R Soc B – Biol Sci* 2015, **282**:20150704.
61. Liang ZS, Nguyen T, Mattila HR, Rodriguez-Zas SL, Seeley TD, Robinson GE: **Molecular determinants of scouting behavior in honey bees.** *Science* 2012, **335**:1225-1228.
62. Liang ZS, Mattila HR, Rodriguez-Zas SL, Southey BR, Seeley TD, Robinson GE: **Comparative brain transcriptomic analyses of scouting across distinct behavioural and ecological contexts in honeybees.** *Proc R Soc B – Biol Sci* 2014, **281**:20141868.
- Previous work (Liang et al. [61]) showed that honey bees that scouted for food also tended to scout for new nest sites, and that scouting behavior was associated with brain gene expression. Here, Liang et al. further investigate gene expression associated with scouting. Both food and nest scouts exhibit similar patterns of glutamate- and GABA-related genes,

but differ in their expression of other genes, such as odour-binding protein 4.

63. Chandrasekaran S, Rittschof CC, Djukovic D, Gu H, Raftery D, Price ND, Robinson GE: **Aggression is associated with aerobic glycolysis in the honey bee brain.** *Genes Brain Behav* 2015, **14**:158-166.
64. Li-Byarlay H, Rittschof CC, Massey JH, Pittendrigh BR, Robinson GE: **Socially responsive effects of brain oxidative metabolism on aggression.** *Proc Natl Acad Sci U S A* 2014, **111**:12533-12537.
65. Toth AL, Tooker JF, Radhakrishnan S, Minard R, Henshaw MT, Grozinger CM: **Shared genes related to aggression, rather than chemical communication, are associated with reproductive dominance in paper wasps (*Polistes metricus*).** *BMC Genomics* 2014, **15**:75.
66. Vargo EL, Leniaud L, Swoboda LE, Diamond SE, Weiser MD, Miller DM, Bagnères AG: **Clinal variation in colony breeding structure and level of inbreeding in the subterranean termites *Reticulitermes flavipes* and *R. grassei*.** *Mol Ecol* 2013, **22**:1447-1462.
67. Fucini S, Uboni A, Lorenzi MC: **Geographic variation in air temperature leads to intraspecific variability in the behavior and productivity of a eusocial insect.** *J Insect Behav* 2014, **27**:403-410.
68. Purcell J, Pellissier L, Chapuisat M: **Social structure varies with elevation in an Alpine ant.** *Mol Ecol* 2015, **24**:498-507.
69. Helms KR, Cahan SH: **Large-scale regional variation in cooperation and conflict among queens of the desert ant *Messor pergandei*.** *Anim Behav* 2012, **84**:499-507.
70. Sheehan MJ, Botero CA, Hendry TA, Sedio BE, Jandt JM, Weiner S, Toth AL, Tibbetts EA: **Different axes of environmental variation explain the presence vs. extent of cooperative nest founding associations in *Polistes paper* wasps.** *Ecol Lett* 2015, **18**:1057-1067.
71. Bengtson SE, Dornhaus A: **Latitudinal variation in behaviors linked to risk tolerance is driven by nest-site competition and spatial distribution in the ant *Temnothorax rugatulus*.** *Behav Ecol Sociobiol* 2015, **69**:1265-1274.
72. Valles SM, Oi DH, Porter SD: **Seasonal variation and the co-occurrence of four pathogens and a group of parasites among monogyne and polygyne fire ant colonies.** *Biol Control* 2010, **54**:342-348.
73. McMahon DP, Furst MA, Caspar J, Theodorou P, Brown MJF, Paxton RJ: **A sting in the spit: widespread cross-infection of multiple RNA viruses across wild and managed bees.** *J Anim Ecol* 2015, **84**:615-624.
74. Brown MJF, Jones CM: **Parasites and genetic diversity in an invasive bumblebee.** *J Anim Ecol* 2014, **83**:1428-1440.
75. Wilkinson EB, Feener DH: **Variation in resource size distribution around colonies changes ant-parasitoid interactions.** *Insect Soc* 2010, **57**:385-391.
76. Gordon DM: **Behavioral flexibility and the foraging ecology of seed-eating ants.** *Am Nat* 1991, **138**:379-411.
77. Ingram KK, Pilko A, Heer J, Gordon DM: **Colony life history and lifetime reproductive success of red harvester ant colonies.** *J Anim Ecol* 2013, **82**:540-550.
78. Richardson T, Gorochoowski T: **Beyond contact-based transmission networks: the role of spatial coincidence.** *J R Soc Interface* 2015, **12**.
79. Denier D, Bulmer MS: **Variation in subterranean termite susceptibility to fatal infections by local *Metarhizium* soil isolates.** *Insect Soc* 2015, **62**:219-226.
80. Fogarty S, Cote J, Sih A: **Social personality polymorphism and the spread of invasive species: a model.** *Am Nat* 2011, **177**:273-287.
81. Sih A, Cote J, Evans M, Fogarty S, Pruitt J: **Ecological implications of behavioural syndromes.** *Ecol Lett* 2012, **15**:278-289.
82. Réale D, Garant D, Humphries MM, Bergeron P, Careau V, Montiglio P-O: **Personality and the emergence of the pace-of-life syndrome concept at the population level.** *Philos Trans R Soc B* 2010, **365**:4051-4063.
83. Harris RJ, Moller H, Winterbourn MJ: **Competition for honeydew between two social wasps in South Island beech forests, New Zealand.** *Insect Soc* 1994, **41**:379-394.
84. Monceau K, Moreau J, Poidatz J, Bonnard O, Thiery D: **Behavioral syndrome in a native and an invasive hymenoptera species.** *Insect Sci* 2015, **22**:541-548.
Vespa crabro (native) foundresses vary greatly within their native range. *Vespa velutina* (invasive) foundresses vary less within the sympatric range of *V. crabro*, but overall their foundresses tend to be more active, bolder, and more exploratory than the native species. These traits may influence their ecological success as invaders.
85. Wang J, Wurm Y, Nipitwattanaphon M, Riba-Grognuz O, Huang Y-C, Shoemaker D, Keller L: **A Y-like social chromosome causes alternative colony organization in fire ants.** *Nature* 2013, **493**:664-668.
86. Lawson LP, Vander Meer RK, Shoemaker D: **Male reproductive fitness and queen polyandry are linked to variation in the supergene *Gp-9* in the fire ant *Solenopsis invicta*.** *Proc R Soc Lond B: Biol Sci* 2012, **279**:3217-3222.
87. Vandermeer RK, Obin MS, Morel L: In *Nestmate Recognition in Fire Ants: Monogyne and Polygyne Populations*. Edited by Vandermeer RK, Jaffe K, Cedeno. Westview Press; 1991:322-328.