FACIAL RECOGNITION: INTRASPECIFIC VARIATION AND DEVELOPMENT OF SPECIALIZATION IN *POLISTES FUSCATUS*, A MODEL SYSTEM

Allison Injaian
Traditional Master's
Ecology and Evolutionary Biology
University of Michigan
May 2013

Thesis Committee Chair: Elizabeth Tibbetts
Committee Members: Thore Bergman, Jacinta Beehner

Testing the development of specialized face learning through
Polistes fuscatus paper wasps, a model system

ABSTRACT

Specialized face learning, the ability to learn and remember faces better than other visual stimuli, occurs across a wide range of social animal taxa. However, the ontogeny of specialized face learning, specifically whether it develops due to innate, learned, or a combination of innate and learned factors, remains debated in the literature. Empirical data on face specialization has supported all three hypotheses, yet conflicting methodologies and data interpretations complicate our understanding of the ontogeny of face specialization. In this study, we use *Polistes fuscatus* (paper wasp), a system with intraspecific variation in developmental environment (innate) and experience (learned), to test the ontogeny of specialized face learning. Our results support the combination hypothesis for the development of specialized face learning, with both innate and learned factors needed to fully explain intraspecific variation in face specialization. Wasps with better early nutritional environment (gynes) learned to discriminate faces more accurately than wasps with poorer nutrition during early development (workers), perhaps due to innate variation in neural structures. Furthermore, older wasps (foundresses) learned faces faster than other stimuli, while younger wasps (gynes) showed no difference in rate of learning between stimuli. We posit that older wasps have greater specialization for learning faces than younger wasps due to higher levels of facial exposure throughout life. Controlled manipulations of early development and adult experience will be useful to provide a more detailed analysis of the ontogeny of specialized face learning. Our results, which suggest that the combined effects of learned and innate factors are necessary to

explain the ontogeny of specialized face learning, may be generalizable to all social animals.

INTRODUCTION

In a wide range of social animal societies, recognizing conspecifics facilitates beneficial social behaviors such as parental care, monogamy, and reciprocal altruism (Searcy and Nowicki 2010). This ability, known as individual recognition, can occur through learning and memory of distinct vocal, visual, or chemical identity signals (e.g. unique vocalizations, facial patterns or chemical profiles). Further, to facilitate fast and accurate recognition of these identity signals specialized recognition abilities may be selected for in social animals. Many species have evolved specialized recognition for informative signals, meaning that some signals are processed differently (e.g. faster and with higher accuracy) than others. Specialized recognition, and especially its ontogeny, is a contentious issue, as there is debate regarding how frequently and under what circumstances it evolves (Pascalis and Kelly 2009). Perhaps the most familiar example of specialized recognition is the ability of humans to learn and remember conspecific faces better than other complex visual pattern (e.g. specialized face learning) (Kanwisher, McDermott et al. 1997).

Specialized face learning is a well-studied form of specialized recognition (Yin 1969). Non-human primates, sheep, and some wasps, have specialized face learning (Perrett, Mistlin et al. 1988, Kanwisher, McDermott et al. 1997, Kendrick 2001, Sheehan and Tibbetts 2011), though the focus of research to date has centered on primates (de

Haan, Humphreys et al. 2002). The ontogeny of specialized face learning remains debated in the literature, perhaps because natural primate populations lack clear variation in early developmental environment and there are ethical dilemmas impeding experimental manipulations of development (de Haan, Humphreys et al. 2002). There are three main hypotheses in the debate: (1) the domain specific hypothesis (innate), (2) the expertise hypothesis (learned), and (3) a combination of both the innate and learned hypotheses (de Haan, Humphreys et al. 2002, Robbins and McKone 2007). The innate hypothesis posits that, from birth, neural structures are specialized to learn and remember faces in social animals (Yin 1969, Kanwisher 2000). However, specialized face learning may also be explained by the expertise hypothesis, which suggests that the recognition abilities of neural structures are originally generic, with specialization developing through increased exposure to face stimuli (Diamond and Carey 1986, Gauthier and Tarr 1997). Finally, individuals may have some level of specialized face learning at birth and specialization continues to increase with face-experience, supporting the "combination" hypothesis (de Haan, Humphreys et al. 2002).

Fuelling much of the debate, research on the development of specialized face learning has supported all three hypotheses. Humans support the innate hypothesis for specialized face learning, with faces being processed differently than other stimuli. This specialized cognitive process is known as holistic processing (an image is perceived as a whole rather than a sum of its parts) (Le Grand, Mondloch et al. 2004). Despite high levels of exposure and expertise for non-face stimuli, humans do not show holistic processing for non-face images, thus supporting the innate hypothesis (Robbins and McKone 2007).

Different experimental methodologies have shown that high levels of exposure to non-face stimuli can produce specialization for other types of images, thus supporting the learned hypothesis (Gauthier and Nelson 2001). For example, humans show specialized learning abilities for non-face stimuli (e.g., cars, birds, etc.) with high levels of exposure to the object-of-expertise (Carey, De Schonen et al. 1992, Gauthier, Skudlarski et al. 2000). Further, older individuals show greater specialization for learning faces as compared to younger individuals, suggesting that face expertise is acquired throughout life (Passarotti, Paul et al. 2003). Previous studies have used data on neural activation from functional Magnetic Resonance Imaging (fMRI) to support both the innate and learned hypotheses, with humans showing greater neural activation when exposed to certain images (e.g. face) as compared to others (e.g. telephone). One challenge associated with these previous studies is that fMRI data may produce ambiguous results. For example, greater neural activation during face exposure, as compared to object exposure, is typically cited as evidence of face specialization, but can be interpreted in other ways (e.g. animate vs. inanimate object viewing) (Kanwisher, McDermott et al. 1997).

There is strong and unambiguous data in support of the "combination" hypothesis. Young Japanese macaques (*Macaca sylvanus*) reared with no face exposure show an innate preference for face images and this preference increases with face exposure, thus displaying both learned and innate components. Macaques that were exposed to only human or only macaque faces after isolated rearing show greater specialization for the species with which they had experience (Sugita 2008). Despite high amounts of research, the debate of the ontogeny of specialized face learning persists. Therefore, new study

systems, specifically those with intraspecific variation in early developmental environment and adult face exposure, should be used to better understand the ontogeny of specialized face learning.

  This study will test the ontogeny of specialized face learning by comparing face learning abilities of *Polistes fuscatus* (paper wasp) across varying developmental environments and experiences. *P. fuscatus* is a useful system to study the ontogeny of specialized face learning for two main reasons. First, and foremost, *P. fuscatus* foundresses (nest-founding queens) are known to have specialized face learning (e.g. learn conspecific faces better than other visual stimuli) (Sheehan and Tibbetts 2011). Second, intraspecific variation in early developmental environment and behavior between castes of *P. fuscatus* allows for simple tests which may identify the factors that affect the development of specialized face learning (Suryanarayanan, Hermanson et al. 2011). Specifically, although workers (non-reproductives) and gynes (potential foundresses) have similar experiences with conspecific faces during early adulthood (e.g. both live in stable nests (Tibbetts 2007)), nutrition varies early on in development (Suryanarayanan, Hermanson et al. 2011).

  In this study, we will test the development of specialized face learning by comparing the abilities of various castes of *P. fuscatus* wasps to differentiate images of normal faces, manipulated faces, and non-face stimuli (Fig.1). This method has previously shown specialized face learning in *P. fuscatus* foundresses and demonstrated a lack of specialized face learning in other closely related *Polistes* species (Sheehan and Tibbetts 2011). If gynes and workers have specialized face learning, we expect wasps to learn pairs of normal face stimuli faster and/or more accurately than non-face and

manipulated face stimuli. Comparisons between normal face and manipulated face stimuli will provide a particularly good test of specialized learning because faces and manipulated faces are composed of the same colors and patterns, but the visual system does not perceive manipulated faces holistically (Fig. 1).

METHODS

Worker and gyne collection

Thirty-five *P. fuscatus* workers were collected from nest boxes at the Matthaei Botanical Gardens in Ann Arbor, Michigan in June and July of 2012, before any males emerged from the nest. Thirty *P. fuscatus* gynes were collected at the Matthaei Botanical Gardens and the E.S. George Reserve in Pinckney, Michigan in August and September of 2012, after male emergence. Nest boxes were checked at least 3 times a week from 6-8 AM for *P. fuscatus* pupae and adults. During each nest census, all wasps on the nest were given unique markings on the dorsal side of the thorax using *Testors* enamel paint. In May, before workers had emerged, all wasps on the nests were considered foundresses (Gamboa, Wacker et al. 1990). Any unpainted wasp that appeared on the nest was assumed to have just recently emerged. This assumption was verified by checking for an open pupae cell, indicating an adult emergence. A record of all emergence dates and unique paint markings was kept to facilitate later identifications of wasps.

Workers and gynes were removed from the nest 10-14 days post-emergence and brought to the Tibbetts lab at the University of Michigan. Within 2 hours of removal from their natal nest, wasps were weighed to the closest 0.01 g, housed in individual

containers, and provided with food and water *ad libitum*. Each wasp began training

between 3 and 8 hours after collection to ensure natural behavior.

Stimuli

Wasps were trained using images that were previously developed to test

specialized face learning in *P. fuscatus* foundresses (Sheehan and Tibbetts 2011). Gynes

and workers were exposed to pairs of normal face, manipulated face, and non-face

stimuli (Fig. 1). Non-face stimuli were comprised of high-contrast black and white

patterns that have been previously shown to be discernable by *P. fuscatus* and accurately

assess general visual learning (Sheehan and Tibbetts 2011, Lehrer and Campan 2004).

Manipulated face stimuli were comprised of pictures of *P. fuscatus* faces in which the

antennae were removed using *Adobe Photoshop*. Manipulated faces robustly produce

differences in recognition ability, as compared to normal faces, in species with

specialized face learning (Sheehan and Tibbetts 2011). Therefore, the removal of

antennae provides a strong control for tests of specialized face learning in *P. fuscatus,* as

the face is no longer perceived holistically.

Training

Wasps were trained to discriminate stimuli in a T-shaped maze that was negatively-

reinforced with mild electric current, approximately 4.5v delivered by a VARIAC

transformer (Fig. 2). Before entering the maze, each wasp was placed in a holding cell at

the base of the "T" and given approximately 5 seconds to adjust to the mild electric

current. After this adjustment period, a door opened allowing the wasp to enter the maze

and choose between two stimuli on either side of the "T." One stimulus was consistently

associated with an unelectrified area of the maze. The side of this "safe-zone" varied

based on a predetermined, pseudo-random order over the 40 trials. Therefore, wasps needed to learn the stimulus associated with the "safe-zone" to avoid the mild electric current. We considered a wasp to have made a choice between the two stimuli once her entire body crossed the threshold of a side chamber. Each trial lasted 2 minutes, however if a wasp did not choose an image within these 2 minutes, she was removed from the maze and given 1 minute to recover before the trial was redone. Correct ("safe-zone" stimulus) and incorrect (electrified stimulus) decisions were recorded over the 40 trials. If a wasp learned, the number of correct choices should be greater than expected by chance and/or increase over time. Also, if a wasp has specialized face learning, we expect higher accuracy and faster learning when exposed to normal faces, as compared to non-face and manipulated face stimuli.

Between each of the 2-minute trials, wasps were placed back into their original housing container and given access to food and water for 10 seconds to allow recovery. During training, 4 gynes and 1 worker showed a side bias by choosing one side of the maze in greater than 70% of the trials (Sheehan and Tibbetts 2011). Data from these wasps were excluded.

Analysis

For each group (normal face, manipulated face, and non-face stimuli) the observed number of correct choices was compared to the randomly expected number of correct choices using χ^2 goodness of fit tests. Tests were done at the $p<0.05$ significance level. By identifying if the observed number of correct choices differed from chance, we identified if learning occurred in any of the stimuli treatments. The last 10 trials were

used to estimate a wasp's ability to discriminate stimuli, as differences between stimuli are expected to be greatest in the last 10 trials.

A Pearson χ^2 test of association was used to compare the number of correct choices in the last 10 trials for: (1) gynes trained to discriminate normal face, non-face, and manipulated face stimuli (2) workers trained to discriminate normal face, non-face, and manipulated face stimuli and (3) gynes and workers trained to discriminate normal face stimuli. Tests were done at the p<0.05 significance level.

Differences in the rates of learning over all 40 trials were assessed using a generalized estimating equation (GEE) for: (1) gynes trained to discriminate normal face, non-face, and manipulated face stimuli (2) workers trained to discriminate normal face, non-face, and manipulated face stimuli, and (3) gynes and workers trained to discriminate normal face stimuli. This GEE tests the speed of learning (based on number of correct choices) for each treatment while taking into account repeated measures. In the model, individual wasp identity was the subject variable and trial number was the within-subject variable. Within-subject dependencies were set as exchangeable since the outcomes of any two trials were assumed to have the same correlation. Tests were done at the p<0.05 significance level.

RESULTS

Workers were unable to learn any of the stimuli, as the number of correct choices did not differ from random chance on any of the three stimuli types (Normal face: Pearson $\chi^2_{0.05,1} = 2.13$, p = 0.144, n = 640; Non-face: Pearson $\chi^2_{0.05,1} = 0.07$, p = 0.791, n =

480; Manipulated face: Pearson $\chi^2_{0.05,1} = 0.72$, p = 0.396, n = 280). By contrast, gynes were more successful learners. Gynes learned to discriminate between pairs of normal face stimuli (Pearson $\chi^2_{0.05,1} = 8.33$, p = 0.0039, n = 400) and non-face stimuli (Pearson $\chi^2_{0.05,1} = 5.95$, p = 0.014, n = 400), but not manipulated faces (Pearson $\chi^2_{0.05,1} = 0.5$, p = 0.480, n = 400). These results suggest that workers are less able to accurately learn visual information, especially faces, as compared to gynes.

Since gynes, but not workers, learn to discriminate normal face and non-face stimuli, the results suggest that castes differ in learning ability. Gynes showed a greater ability to discriminate normal face stimuli than workers, thus showing a difference in facial recognition abilities between castes (Pearson $\chi^2_{0.05,1} = 3.71$, p = 0.054, n = 260). Gynes also discriminate non-face stimuli more accurately than workers, thus suggesting variation in general visual recognition between castes (Pearson $\chi^2_{0.05,1} = 7.75$, p = 0.005, n = 220). However, workers and gynes trained to discriminate manipulated face stimuli showed similar recognition abilities (Pearson $\chi^2_{0.05,1} = 0.08$, p = 0.777, n =170).

Further, the presence of face specialization differed across castes. Gynes showed specialized face learning, as they learned to discriminate normal face images more accurately than manipulated face images (Pearson $\chi^2_{0.05,1} = 4.8$, p = 0.028, n = 200). In contrast, workers were not specialized for face learning, as they failed to learn both normal faces and manipulated faces (Pearson $\chi^2_{0.05,1} = 0.02$, p = 0.888, n = 230).

Although accuracy differed across castes and stimuli, neither gynes or workers showed differences in the rate of learning between normal face, non-face, and manipulated face stimuli (GEE Gyne model: Wald $\chi^2_{0.05,2} = 3.034$, p = 0.219, n = 1200; GEE Worker model: Wald $\chi^2_{0.05,2} = 2.035$, p = 0.361, n = 1400)(Fig. 3A and B). Further,

no differences were found between workers and gynes for the rate of learning of normal face stimuli (GEE model: Wald $\chi^2_{0.05,1}$ = 1.655, p = 0.198, n = 1040)(Fig.3C).

DISCUSSION

We were able to identify that both early nutritional environment (innate) and face exposure (learned) factors are needed to fully explain the development of specialized face learning in *P fuscatus* paper wasps. Therefore, the results of this study support the "combination" hypothesis of specialized face learning. We found significant intraspecific variation in specialized face learning in *P. fuscatus*, with gynes showing greater face and visual processing than workers. Specifically, gynes were significantly better at learning normal face and non-face stimuli than workers. Our results add to previous work suggesting that, like humans and other primates, *P. fuscatus* paper wasps use specialized holistic processing for face images: minor manipulations to face stimuli (e.g., removal of antennae) disrupt holistic processing and prevent gynes from successfully discriminating between images (Le Grand, Mondloch et al. 2004).

The innate differences in learning between gynes and workers may be caused by variation in early nutritional environment. Compared to workers, gynes emerge from the nest with greater stores of fat due to better nutrition during early development (Suryanarayanan, Hermanson et al. 2011). This increased energy supply allows gynes to survive the winter, however it may also be related to innate differences in neural structures between castes (Molina, Harris et al. 2009). Since neural structures are energetically costly to produce and maintain, the increased fat stores available to gynes

may facilitate the formation of a brain that is capable of greater face learning abilities than workers (Burns, Foucaud et al. 2011). The effects of early nutritional environment on recognition may be generalizable, as they have been found in honeybees and rats. Honeybee birth weight is positively correlated with innate olfactory learning ability and rats with poor early nutritional environment show permanently reduced neural cell size and number, which decreases innate spatial memory (Nowicki, Searcy et al. 2002, Scheiner 2012). Future studies should further test the effect nutrition on the development of innate face learning abilities, through controlled manipulations of food availability during early development of *P. fuscatus*.

The reduced learning abilities of *P. fuscatus* workers, as compared to reproductive gynes, may be related to cost-benefit trade-offs. Specialized face learning is associated with energetic costs, such as the formation of specialized neural structures (Burns, Foucaud et al. 2011). In gynes these costs are offset by social benefits, such as decreased aggression (Tibbetts 2002, Sheehan and Tibbetts 2009). After gynes emerge from diapause (now considered foundresses), they use either of two strategies during the nest-founding period; 1) build a nest of their own 2) forgo nest-building and join the nest of another foundress as a cooperative partner. When a potential cooperative partner first lands on the nest of another foundress she is met with high levels of aggression from the nest-owner, as the nest-owner needs to establish her dominance and ensure the egg-laying rights on the nest (Cant, English et al. 2006). The ability to learn and remember the facial pattern of previously encountered partners allows foundresses to avoid aggression during successive encounters (Sheehan and Tibbetts 2009). These benefits, which likely led to the evolution of individual recognition and specialized face learning, are suggested to be

received only by foundresses and occur only during the nest-founding period (Tibbetts and Sheehan 2013). Although workers are capable of individual recognition, current data suggests that workers do not receive benefits from visual face recognition during the nest founding stage or later stages (Tibbetts 2002). Workers have not yet emerged during the nest-founding and are suggested to use chemical, rather than visual, cues to identify and avoid aggression from the dominant reproductive in later nest stages (Haggard and Gamboa 1980, Tibbetts 2002). Therefore, the social benefits associated with specialized face learning may not outweigh the costs for *P. fuscatus* workers and may not favor specialized face learning.

Interestingly, comparisons of this data with previous research show that there are differences in learning across gyne and foundress *P. fuscatus* (Sheehan and Tibbetts 2011). Gynes become foundresses after overwintering, so the two groups only differ in experience. Yet, foundresses are highly specialized and learn faces faster than any other visual stimuli, while gynes show no difference in the rate of learning between stimuli (Sheehan and Tibbetts 2011). Further, foundresses collected from the same *P. fuscatus* population and tested using the same experimental methodology as this study were approximately 75% accurate at discriminately facial images, while gynes were showed only 58% accuracy. Varying early nutritional environments, which we propose explains specialization differences between *P. fuscatus* gynes and workers, is not sufficient to explain learning differences between gynes and foundresses, as they have the same early developmental environment (Gamboa, Wacker et al. 1990). Therefore, we posit that foundresses (approximately 8 months old) have greater specialized face learning than gynes (approximately 2 weeks old) due to higher levels of face exposure. Foundresses

have had high levels of social interaction both on the nest and off the nest in pre-hibernation clusters (Dapporto and Palagi 2006). Experience also affects recognition abilities in damselflies (*Enallagma boreale*), with individuals from areas with northern pike (*Esox lucius*), a predatory fish, showing greater specialized predator recognition as compared to individuals from areas where pike do not occur (Wisenden, Chivers et al. 1997). To further test the role of experience in the development of specialized face learning future studies should experimentally rear *P. fuscatus* wasps with minimal exposure to phenotypically variable faces. For example, rearing *P. fuscatus* on the nest of *P. metricus*, a closely related and behaviorally similar species that lacks highly variable facial patterns and face specialization, could serve as a powerful test of the effect of face exposure on specialization.

Conclusion

Our results support findings of specialized face learning *P. fuscatus* paper wasps and suggest that both learned and innate factors contribute to the ontogeny specialized face learning. *P. fuscatus* paper wasps provide a highly useful system for studying the ontogeny of face specialization, as more detailed research can be completed with relative ease through manipulations of early nutritional environment and levels of face exposure.

ACKNOWLEDGMENTS

Figures

Figure 1. Training images used to test specialized facial recognition abilities of *P. fuscatus* gynes and workers; A) normal face, B) manipulated (antennae-less) face, and C) non-face (pattern) stimuli.
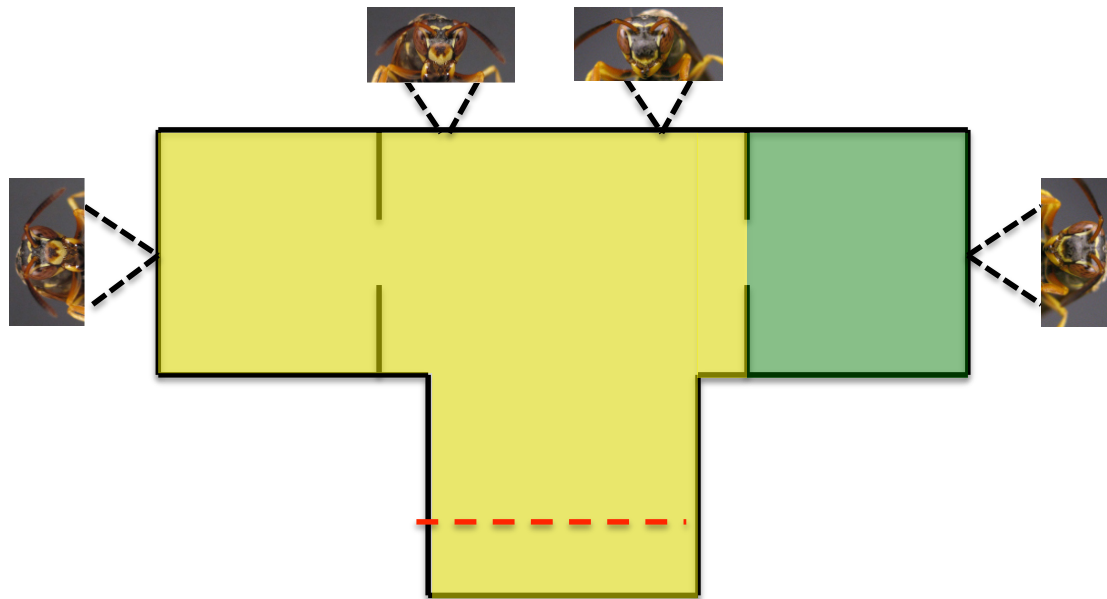

Figure 2. T-shaped maze used to train *P. fuscatus* wasps. The electrified (4.5v) portion of the maze is shaded in yellow and the "safe-zone" is shaded in green. The red dotted line depicts the "door," which was removed to allow wasps to enter the maze after the 10 s adjustment period. Stimuli were approximately life-size and placed vertically in the locations depicted above, allowing wasps to view images "head on."
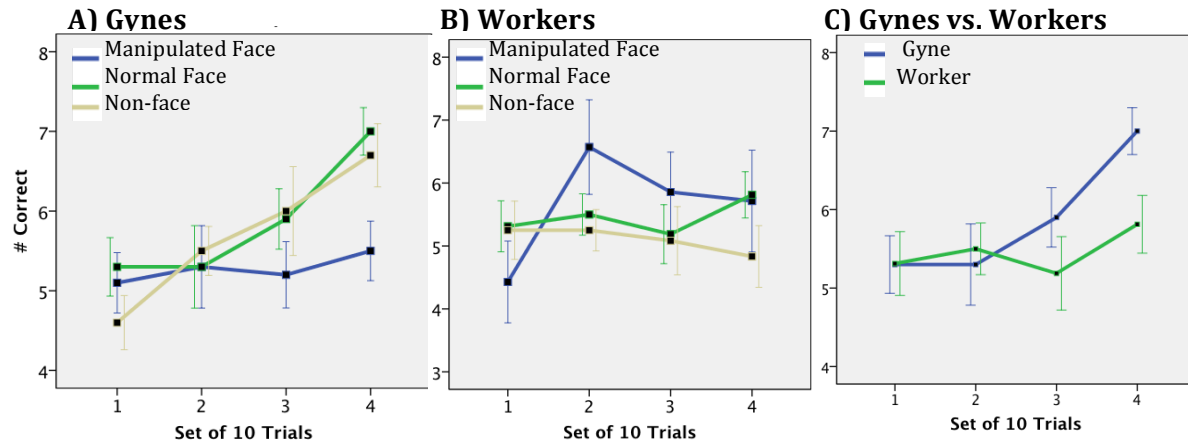
Figure 3. Mean number of correct choices (+/- 1 SE) in each set of 10 trials for a) gynes trained to discriminate normal face, manipulated face, and non-face stimuli. b) workers trained to discriminate normal face, manipulated face, and non-face stimuli. C) gynes and workers trained to discriminate normal face stimuli. Random choice is approximated at 5 correct choices per set of 10 trials.

References

Burns, J. G., J. Foucaud and F. Mery (2011). "Costs of memory: lessons from

‘mini’brains." Proceedings of the Royal Society B: Biological Sciences

278(1707): 923-929.

Cant, M. A., S. English, H. K. Reeve and J. Field (2006). "Escalated conflict in a social

hierarchy." Proceedings of the Royal Society B-Biological Sciences

273(1604): 2977-2984.

Carey, S., S. De Schonen and H. Ellis (1992). "Becoming a Face Expert [and

Discussion]." Philosophical Transactions of the Royal Society of London.

Series B: Biological Sciences **335**(1273): 95-103.

Dapporto, L. and E. Palagi (2006). <u>Wasps in the shadow: looking at the pre-hibernating clusters of Polistes dominulus</u>. Annales Zoologici Fennici, Helsinki: Suomen Biologian Seura Vanamo, 1964-.

de Haan, M., K. Humphreys and M. H. Johnson (2002). "Developing a brain specialized for face perception: A converging methods approach." <u>Developmental Psychobiology</u> **40**(3): 200-212.

Diamond, R. and S. Carey (1986). "Why faces are and are not special: an effect of expertise." <u>Journal of Experimental Psychology: General; Journal of Experimental Psychology: General</u> **115**(2): 107.

Gamboa, G. J., T. L. Wacker, J. A. Scope, T. J. Cornell and J. Shellman-Reeve (1990). "The Mechanism of Queen Regulation of Foraging by Workers in Paper Wasps (Polistes fuscatus, Hymenoptera: Vespidae)." <u>Ethology</u> **85**(4): 335-343.

Gauthier, I. and C. A. Nelson (2001). "The development of face expertise." <u>Current opinion in neurobiology</u> **11**(2): 219-224.

Gauthier, I., P. Skudlarski, J. C. Gore and A. W. Anderson (2000). "Expertise for cars and birds recruits brain areas involved in face recognition."

Gauthier, I. and M. J. Tarr (1997). "Becoming a" Greeble" expert: exploring mechanisms for face recognition." <u>Vision research</u> **37**(12): 1673-1682.

Gauthier, I., M. J. Tarr, J. Moylan, P. Skudlarski, J. C. Gore and A. W. Anderson (2000). "The fusiform "face area" is part of a network that processes faces at the individual level." Journal of Cognitive Neuroscience **12**(3): 495-504.

Haggard, C. M. and G. J. Gamboa (1980). "Seasonal variation in body size and reproductive condition of a paper wasp, Polistes metricus (Hymenoptera: Vespidae)." The Canadian Entomologist **112**(03): 239-248.

Kanwisher, N. (2000). "Domain specificity in face perception." Nature neuroscience **3**: 759-763.

Kanwisher, N., J. McDermott and M. M. Chun (1997). "The fusiform face area: a module in human extrastriate cortex specialized for face perception." The Journal of Neuroscience **17**(11): 4302-4311.

Kendrick, K. M., da Costa, A. P., Leigh, A. E., Hinton, M. R., and Peirce, J. W. (2001). "Sheep don't forget a face." Nature **414**: 165-166.

Le Grand, R., C. J. Mondloch, D. Maurer and H. P. Brent (2004). "Impairment in holistic face processing following early visual deprivation." Psychological Science **15**(11): 762-768.

Lehrer, M. and R. Campan (2004). "Shape discrimination by wasps (Paravespula germanica) at the food source: generalization among various types of contrast." Journal of Comparative Physiology A **190**(8): 651-663.

Molina, Y., R. Harris and S. O'Donnell (2009). "Brain organization mirrors caste differences, colony founding and nest architecture in paper wasps (Hymenoptera: Vespidae)." Proceedings of the Royal Society B: Biological Sciences **276**(1671): 3345-3351.

Nowicki, S., W. A. Searcy and S. Peters (2002). "Brain development, song learning and mate choice in birds: a review and experimental test of the "nutritional stress hypothesis"." Journal of Comparative Physiology a-Neuroethology Sensory Neural and Behavioral Physiology **188**(11-2): 1003-1014.

Pascalis, O. and D. J. Kelly (2009). "The origins of face processing in humans: Phylogeny and ontogeny." Perspectives on Psychological Science **4**(2): 200-209.

Passarotti, A. M., B. M. Paul, J. R. Bussiere, R. B. Buxton, E. C. Wong and J. Stiles (2003). "The development of face and location processing: an fMRI study." Developmental Science **6**(1): 100-117.

Perrett, D., A. Mistlin, A. Chitty, P. Smith, D. Potter, R. Broennimann and M. Harries (1988). "Specialized face processing and hemispheric asymmetry in man and monkey: evidence from single unit and reaction time studies." Behavioural brain research **29**(3): 245-258.

Robbins, R. and E. McKone (2007). "No face-like processing for objects-of-expertise in three behavioural tasks." Cognition **103**(1): 34-79.

Scheiner, R. (2012). "Birth weight and sucrose responsiveness predict cognitive skills of honeybee foragers." Animal Behaviour **84**(2): 305-308.

Searcy, W. A. and S. Nowicki (2010). The Evolution of Animal Communication: Reliability and Deception in Signaling Systems: Reliability and Deception in Signaling Systems, Princeton University Press.

Sheehan, M. J. and E. A. Tibbetts (2009). "Evolution of identity signals: frequency-dependent benefits of distinctive phenotypes used for individual recognition." Evolution **63**(12): 3106-3113.

Sheehan, M. J. and E. A. Tibbetts (2011). "Specialized face learning is associated with individual recognition in paper wasps." science **334**(6060): 1272-1275.

Sherman, P. W., H. K. Reeve and D. W. Pfennig (1997). "Recognition systems." Behavioural ecology: an evolutionary approach: 69-96.

Sugita, Y. (2008). "Face perception in monkeys reared with no exposure to faces." Proc Natl Acad Sci U S A **105**(1): 394-398.

Suryanarayanan, S., J. C. Hermanson and R. L. Jeanne (2011). "A mechanical signal biases caste development in a social wasp." Current Biology **21**(3): 231-235.

Tibbetts, E. A. (2002). "Visual signals of individual identity in the wasp Polistes fuscatus." Proceedings of the Royal Society of London. Series B: Biological Sciences **269**(1499): 1423-1428.

Tibbetts, E. A. (2007). "Dispersal decisions and predispersal behavior in Polistes paper wasp 'workers'." Behavioral Ecology and Sociobiology **61**(12): 1877-1883.

Wisenden, B. D., D. P. Chivers and R. J. F. Smith (1997). "Learned recognition of predation risk by Enallagma damselfly larvae (Odonata, Zygoptera) on the basis of chemical cues." Journal of Chemical Ecology **23**(1): 137-151.

Yin, R. K. (1969). "Looking at upside-down faces." Journal of experimental psychology **81**(1): 141.

CHAPTER 2

Cognition across castes: Individual recognition in worker
Polistes fuscatus wasps

ABSTRACT

In many signaling systems, intraspecific variation in recognition abilities is based on developmental stage, experience, or caste. However, the occurrence of intraspecific variation in recognition has not been thoroughly examined in species with individual recognition. For example, previous work has shown that individual recognition is an important aspect of the social life of *Polistes fuscatus* (paper wasp) nest founding queens, as individual recognition stabilizes dominance interactions and reduces aggression. Yet, to date the potential for individual recognition among *P. fuscatus* workers has been largely ignored. Here, we explore whether there is intraspecific variation in individual recognition by testing *P. fuscatus* worker recognition abilities in a series of staged contests. The results indicate that *P. fuscatus* workers are capable of individual recognition: focal workers paired with previously encountered partners experienced significantly less aggression and more nonaggressive bodily contact than focal workers paired with unknown social partners. Therefore, this study finds no evidence of intraspecific variation in individual recognition across castes of *P. fuscatus*. We propose two potential explanations for individual recognition among workers: 1) worker individual recognition may be favored because it provides social benefits to workers, or 2) worker individual recognition may be a byproduct of selection for individual recognition in foundresses. Individual recognition is often considered a cognitively challenging form of recognition, so future studies that compare the sophistication of recognition across castes will be useful to assess whether there are more subtle differences in cognitive abilities or recognition behavior between *P. fuscatus* nest-founding queens and workers.

Key words: intraspecific variation, individual recognition, social behavior

INTRODUCTION

Animals exhibit a range of recognition behaviors, including species, gender, kin, mate, and individual recognition (Sherman 1997). Individual recognition is a relatively precise form of recognition where each social partner is identified through its unique phenotype (Dale 2001). Individual recognition is typically considered to be more cognitively complex than many other forms of recognition as it requires organisms to learn and remember the distinctive phenotypes of multiple conspecifics (Barnard & Burke 1979). Despite its cognitive complexity, individual recognition is taxonomically widespread, occurring in mammals, birds, lizards, crustaceans, and insects (Sugita 2007; Falls 1982; Glinski & Krekorian 1982; Gherardi et al. 2010; Tibbetts 2002). Individual recognition is also an important factor in many social behaviors, including monogamy, dominance hierarchies, and reciprocal altruism (Muller et al. 2003; Barnard & Burk 1979; Trivers 1971).

To date, most research on individual recognition has focused on identifying species that are capable of individual recognition, without assessing whether there is intraspecific variation in recognition abilities (Hurst 2001; Irvine 1998; Brooks 1975). Intraspecific variation in recognition abilities may commonly occur when some receivers are less capable of recognition than others (Reeve 1989). For example, intraspecific variation in kin recognition of red-legged frogs (*Rana aurora*) is based on developmental

stage, with recognition abilities present during larval stages and lost in later life stages (Blaustein & O'Hara 1986). Intraspecific variation in recognition may also be based on experience. For example, juvenile Barbary macaques (*Macaca sylvanus*) cannot distinguish between group and non-group conspecifics, but adults are capable of group discrimination (Schell et al. 2011). Finally, previous work suggests that recognition abilities may commonly vary with caste. For example, nestmate recognition in leaf-cutting ants (*Atta vollenweidei*) varies among worker subcastes, with foraging workers showing increased recognition relative to other worker subcastes (Kuebler et al. 2009). Given the prevalence of intraspecific variation in recognition across species and signaling systems, it may also occur in species with individual recognition.

This study will test the occurrence of intraspecific variation in individual recognition by testing individual recognition across castes in *Polistes fuscatus* paper wasps. Previous work has shown that *P. fuscatus* nest-founding queens have variable facial patterns that are used for individual recognition (Tibbetts 2002). Queens are quite adept at individual recognition, as they remember individual conspecifics after a separation of at least a week, even if they are living in a complex social environment with multiple other individuals (Sheehan & Tibbetts 2008). *P. fuscatus* queens also have cognitive specialization for individual face recognition, as they learn faces faster and more accurately than other types of visual stimuli (Sheehan & Tibbetts 2011). Much less is known about the extent of individual recognition in worker *P. fuscatus*. Tibbetts (2002) found that workers, which also have highly variable facial patterns (Fig. 1), are likely capable of individual face recognition, though the pattern was only significant with a one-

tailed statistical analysis. There have been no previous tests of individual recognition and memory in *P. fuscatus* workers.

It is difficult to predict the extent of individual recognition in *P. fuscatus* workers. Previous experimental and comparative work suggests that individual recognition evolved to reduce costly aggressive interactions among nest-founding queens (foundresses) (Tibbetts 2002; Sheehan & Tibbetts 2009). Behavioral experiments have shown that there are substantial social benefits associated with individual recognition in foundresses, as recognizable foundresses receive less aggression than unrecognizable foundresses (Sheehan & Tibbetts 2009). Further, comparative analyses indicate that the type of variable facial patterns used during social signaling are only found in paper wasp species that form cooperative foundress associations, suggesting that individual recognition is favored due to social benefits in the founding stage (Tibbetts 2004; Sheehan & Tibbetts 2010). Although individual recognition is important among foundresses, there is no evidence that workers use individual recognition. Worker-queen social interactions are thought to involve chemical signaling rather than individual recognition (Pfennig et al. 1983; Tibbetts & Sheehan 2013). As there is no clear selective benefit associated with individual recognition in workers, workers may be less able to learn and remember individual conspecifics than foundresses (Tibbetts 2002). At the same time, *Polistes* are primitively eusocial insects: they lack discrete pre-imaginal castes (Michener 1969; Michener 1974; O'Donnell 1998). Queens and workers appear morphologically similar and behavior is flexible (Reeve 1991). For example, although most of the first brood to emerge on a nest are non-reproductive foragers (workers), a few

start their own nests or enter early diapause and emerge the following year as nest-founding queens (O'Donnell 1996). There may be sufficient overlap between foundresses and workers that workers are capable of individual recognition, even if individual recognition is not specifically favored in the worker context.

This study will test individual recognition in *P. fuscatus* workers through a series of staged contests between wasps. Similar methods have been used previously to test individual memory in *P. fuscatus* and to demonstrate a lack of individual recognition in *P. dominulus* and *P. metricus* (Sheehan & Tibbetts 2008; Sheehan & Tibbetts 2010). If *P. fuscatus* workers are capable of individual recognition, we expect workers to treat known and unknown rivals differently. Specifically, we predict more aggression and fewer non-aggressive interactions (positive social behavior) between wasps during their first meeting than between wasps with prior social interactions (Drier et al. 2007; Sheehan & Tibbetts 2008).

METHODS

Worker collection

P. fuscatus were collected from nest boxes at the Matthaei Botanical Gardens in Ann Arbor, Michigan in June and July of 2012. Nest boxes were checked daily from 6-8AM for the presence of *P. fuscatus* pupae and adults. We considered wasps to be foundresses if they were on the nest at the beginning of the nest-founding season, before

workers emerged (Gamboa et al. 1990). Foundresses were given individual markings on the dorsal side of the thorax using *Testors* enamel paint, and then placed back on their nest (Sheehan & Tibbetts 2008). Since foundresses forage during the nest-founding period, nests were checked early in the morning when all nest members were present. We considered wasps to be workers if they appeared on the nest unpainted, the nest showed signs that a pupae had emerged (the white film covering on pupal cell was broken open) and the nest had not yet produced male wasps. Newly-identified workers were briefly removed from the nest and given a unique paint marking.

On day 10 post-emergence, workers were removed from the nest and brought back to the Tibbetts lab at the University of Michigan. Within 2 hours of collection, wasps were weighed to the closest 0.01g, housed in individual containers, and provided with food and water *ad libitum*. Each wasp remained in the lab for at least 3 days prior to experimental procedures.

Experimental video setup

We assessed the recognition abilities of *P. fuscatus* workers by staging contests between pairs of wasps with and without a prior history of social interactions. During these contests, the occurrence and intensity of aggressive interactions were scored, as well as displays of non-aggressive behavior. Natal nests of paired *P. fuscatus* were at least 10m apart to reduce the probability that partner wasps had encountered each other in the wild. Any previous wild interactions between paired workers would reduce the

probability of measuring individual recognition in the lab. We believe 10m is sufficient

separation due to behavioral surveys, which suggest that workers may occasionally drift

between adjacent nests (3m), but rarely interact over longer distances (Sumner et al.

2007).

Focal wasps were paired with known and unknown partner wasps over four days

and interactions were recorded and analyzed. Start date was staggered across trials to

ensure that differences in behavior across days were caused by experimental treatment

rather than day-specific effects. In the first trial (day 0), two workers with no previous

encounters were placed in a small container and their interactions were filmed. After

filming, these wasps were housed together until the next day (day 1) at which point they

were separated and returned to their initial solitary housing. One day later, the same two

wasps were filmed interacting again (day 2). To ensure that any changes in aggression

between days 0 and 2 were a result of recognition and not of decreases in motivation over

time, we paired the wasps with other unknown social partners on the day before and after

(days 1 and 3). On day 1, wasps were housed individually for approximately 5 h between

separation from their initial partner and meeting a new partner. If the wasps are able to

recognize and remember social partners, they should be least aggressive when they

interact with a known individual (day 2) (e.g., Sheehan & Tibbetts 2008). Species

capable of individual recognition behave differently towards individuals with whom they

share a history of prior interactions (Barnard & Burke 1979). In this case, species with

individual recognition are predicted to be less aggressive towards the individual they

have previously encountered (day 2) than towards individuals they are encountering for the first time (days 0, 1 and 3) (Drier et al. 2007; Sheehan & Tibbetts 2008).

Scoring tapes

Cooperative and aggressive behaviors were ranked as follows; (0) bodily contact without aggression (1) dart (2) dart with open mandibles (3) bite (4) grapple/mount (West-Eberhard 1969; Dreier et al. 2007; Sheehan & Tibbetts 2008). For each tape, the ranks of cooperative and aggressive behaviors were summed. This sum was divided by the number of total interactions per tape to calculate an aggression index (Dreier et al. 2007). The aggression index standardized behavior by taking into account the number and intensity of interactions of each pair, which allowed behavior to be compared across trials.

Analysis

Data were analyzed using *IBM SPSS v. 20.* Aggression index was compared across trials using a mixed linear model. Day and focal wasp were the independent variables and aggression index was the dependent variable. Focal wasp was included as a random effect in the model to control for any similarity within trials with the same focal wasp. A posthoc Least Significant Difference (LSD) was used for pairwise comparison of aggressive behaviors (aggression or non-aggressive bodily contact) across days**,** showing

significance at the $P < 0.05$ level. The procedure listed above was repeated, using non-aggressive bodily contact as the dependent variable.

RESULTS

Aggression index varied between known and unknown pairings, with the lowest aggression index values on days with a known partner ($F_3 = 8.326$, $P < 0.001$) (Fig. 2A). Pairs of known individuals exhibited significantly less aggression than pairs of unknown individuals (LSD pairwise comparisons days 0 vs. 2, $P = 0.004$; days 1 vs. 2, $P < 0.001$; days 3 vs. 2, $P = 0.002$). Notably, there was no significant difference in aggression across trials with pairs of unknown rivals (LSD pairwise comparisons days 0 vs. 1, $P = 0.059$; days 0 vs. 3, $P = 0.789$; days 1 vs. 3 $P = 0.103$). Therefore, workers visually recognized partners with whom they had previously established a dominance relationship, allowing aggression to be avoided during successive encounters.

Non-aggressive bodily contact (positive social interactions) varied between known and unknown pairings, with the highest values occurring with a known partner ($F_3 = 3.265$, $P = 0.027$) (Fig. 2B). There was significantly more non-aggressive bodily contact between pairs of known individuals than pairs of unknown individuals (LSD pairwise comparisons days 0 vs. 2, $P = 0.036$; days 1 vs. 2, $P = 0.048$; days 3 vs. 2, $P = 0.004$). However, there were no significant differences in non-aggressive contact across trials with pairs of unknown rivals (LSD pairwise comparisons days 0 vs.1, $P = 0.900$; days 0 vs. 3, $P = 0.381$; days 1 vs. 3, $P = 0.318$). Therefore, workers visually recognized

partners with whom they had previously established a dominance relationship, resulting in increased social behavior during successive encounters.

DISCUSSION

The significantly lower aggression and higher levels of non-aggressive contact among known individuals (day 2) than among unknown individuals (days 0, 1 and 3), indicates that *P. fuscatus* workers are capable of individual recognition (Fig. 2). Aggression indices on day 0 and day 3 were not significantly different, thus eliminating decreased aggression over time as a possible explanation for reduced aggression on day 2. The pattern of aggression identified in *P. fuscatus* workers mirrors behavior of *P. fuscatus* foundresses (Sheehan & Tibbetts 2008), suggesting individual recognition occurs in both workers and foundresses. In contrast, the pattern of aggression is entirely different in paper wasp species that lack individual recognition, as wasps from species that lack individual recognition treat known and unknown individuals similarly (Sheehan & Tibbetts 2010).

Although *P. fuscatus* workers can individually recognize conspecifics, the sophistication of individual recognition among workers remains unknown. This experiment illustrates that workers can recall another worker after being separated for one day, however no data on the robustness of individual recognition or specialized face learning has been collected. Future experiments should test the extent of individual recognition in workers, thus providing a comparison to foundress recognition abilities.

Foundresses can remember individual conspecifics for at least a week, even when they are living in a complex social environment (Sheehan & Tibbetts 2008). Further, foundresses are specialized for face learning, as they learn faces better than other visual information (Sheehan & Tibbetts 2011).

Regardless of the level of sophistication, it is interesting that workers are capable of individual recognition. Previous work has identified substantial energy costs associated with learning and memory, both of which are necessary for individual recognition (Dukas 2008; Niven & Laughlin 2008). Specifically, learning and memory increase expenditures of energy, time and resources, as compared to innate behavioral responses (Dukas 2008; Burns et al. 2011). For example, expression of learning induces fitness costs in fruit flies (*Drosophila melanogaster*), with conditioned individuals showing a decrease in fecundity by 40%, as compared to flies from the same line that were not conditioned (Mery & Kawecki 2004). Further, constitutive costs may be associated with the neural structures required for learning and memory (Burns et al. 2011). For example, foundresses of *Polistes* spp. that use facial patterns for recognition have larger neural structures (antennal lobes and mushroom body calyces and lobes) compared to queens of *Polistes* spp. that do not use facial cues (Gronenberg et al. 2008). Development and maintenance of these neural structures is energetically costly, creating a fitness trade-off with other selective traits (Dukas 1999; Burns et al. 2011). Given the substantial costs associated with learning and memory, why do *P. fuscatus* workers recognize individual conspecifics?

There are two potential explanations for the occurrence of individual recognition among workers: (1) individual recognition in workers may be selected because it provides social benefits to workers or (2) individual recognition in workers may be a byproduct of selection for individual recognition in foundresses.

First, there may be benefits associated with individual recognition in workers. Previous work on the evolution of individual recognition in wasps has focused on the benefits associated with individual recognition in foundresses, but workers could also use individual recognition during social interactions (Tibbetts 2002; Tibbetts & Dale 2007; Sheehan & Tibbetts 2008). In particular, *P. fuscatus* workers form linear dominance hierarchies, with substantial aggression between closely ranked workers and theoretical work suggests that individual recognition may commonly stabilize dominance hierarchies (Dugatkin & Earley 2004).

Alternatively, individual recognition among workers may be a byproduct of selection for individual recognition among foundresses. The primitively eusocial *P. fuscatus* lack discrete pre-imaginal castes. Instead, caste is thought to be influenced by a combination of early development and adult social environment (Michener 1969; Michener 1974; O'Donnell 1996). As a result, queens and workers are morphologically similar and there is flexibility in behavioral roles. For example, although most of the first brood to emerge on *P. fuscatus* nests become non-reproductive workers, a few individuals enter early diapause to become nest-founding queens the following year

(Reeve et al. 1998). Therefore, the morphological and behavioral overlap between castes in *P. fuscatus* may account for the occurrence of individual recognition in workers.

Although this study found no evidence for variation in recognition across *P. fuscatus* foundresses and workers, intraspecific variation in individual recognition is likely to be common in other taxa. Intraspecific variation may be especially common in species with larger intraspecific variation in ontogeny and/or behavior such as eusocial insects with discrete, pre-imaginal castes. For example, leaf-cutter ants (*Atta vollenweideri*) have pre-imaginal castes and the forager subcaste has increased trail-pheromone recognition relative to other subcastes. The leaf-cutter ant caste is also associated with morphological and neuroanatomical polyphenism (Kuebler et al. 2009). Further, intraspecific variation in recognition may also be common in species with metamorphosis. For example, kin recognition is important in tadpoles of the red-legged frog (*Rana aurora*), but lost in adulthood, perhaps due to decreased selective benefits associated with anti-predator kin aggregations in adults relative to tadpoles (Blaustein & O'Hara 1986).

Conclusions

Intraspecific variation in recognition is quite common across a wide range of recognition systems, but the possibility of intraspecific variation has been largely ignored in species with individual recognition. Given the relative cognitive complexity and cost of individual recognition, substantial intraspecific differences in recognition may be

widespread. However, this study found that both worker and foundress *P. fuscatus* are capable of individual recognition. The similarity in recognition within *P. fuscatus* is striking and suggests there may be either social benefits associated with individual recognition in workers or developmental limitations that maintain cognitive similarity across castes. Although, there may be intraspecific variation in the expression of the individual recognition: workers may not use individual recognition in all worker-worker and worker-queen contexts (Tibbetts 2002). Future research will be useful to establish whether there are more subtle differences across castes. Such studies could include more detailed comparisons of cognition and neuroanatomy across castes as well as behavioral studies that test the sophistication of individual recognition in workers and foundresses.
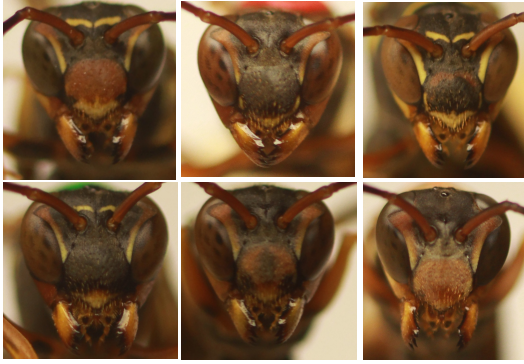
ACKNOWLEDGMENTS

FIGURES

Figure 1. Facial variation of *P. fuscatus* collected in areas surrounding Ann Arbor, Michigan, USA. Facial variation used for individual recognition within *P. fuscatus* is on clypeus, eyebrow, and inner eye.
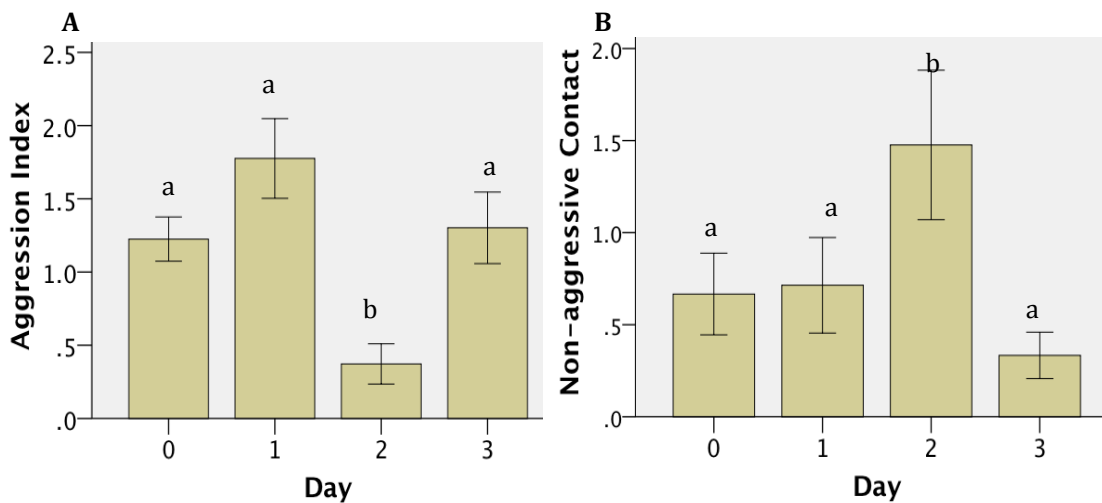

Figure 2. Mean +/- 1 SE a) aggression index and b) non-aggressive contacts per day shown by EMM. On days 0, 1, and 3 focal wasps interacted with individuals that were not previously encountered. On day 2, wasps interacted with a previously encountered partner. Letters (a, b) reflect significant differences ($P < 0.05$).

REFERENCES

Barnard, C. J., & Burk, T. 1979. Dominance hierarchies and the evolution of
"individual recognition." *Journal of Theoretical Biology*, **81**, 65-73.

Blaustein, A. R., & O'Hara, R. K. 1986. An investigation of kin recognition in Red-
legged frog (*Rana aurora*) tadpoles. *Journal of Zoology,* **209,** 347-353.

Brooks, R. J., & Falls, J. B. 1975. Individual recognition by song in white-throated
sparrows. I. Discrimination of songs of neighbors and strangers. *Canadian
Journal of Zoology*, **53**, 879-888.

Burns, J. G., Foucaud, J., & Mery, F. 2011. Costs of memory: lessons from
'mini'brains. *Proceedings of the Royal Society B: Biological Sciences,* **278**, 923-
929.

Dale, J., Lank, D. B., & Reeve, H. K. 2001. Signaling individual identity versus quality:
a model and case studies with ruffs, queleas, and house finches. *The American
Naturalist,* **158**, 75-86.

Dreier, S., van Zweden, J. S. & D'Ettorre, P. 2007. Long-term memory of individual
identity in ant queens. *Biology Letters,* **3**, 459–462.

Dugatkin, L. A., & Earley, R. L. 2004. Individual recognition, dominance hierarchies and winner and loser effects. *Proceedings of the Royal Society of London. Series B: Biological Sciences,* **27**, 1537-1540.

Dukas, R. 1999. Costs of memory: ideas and predictions. *Journal of Theoretical Biology,* **197**, 41-50.

Dukas, R. 2008. Evolutionary biology of insect learning *Annual Review of Entomology*, **53**, 145-160.

Falls, J. B. 1982. Individual recognition by sounds in birds. *Acoustic Communication in Birds,* **2**, 237-278.

Gamboa, G. J., Wacker, T. L., Scope, A. J., Cornell, T. J. & Shellman-Reeve, J. 1990. The mechanism of queen regulation of foraging in paper wasps (*Polistes fuscatus*, Hymenoptera: Vespidae). *Ethology,* **85**, 335–343.

Gherardi, F., Cenni, F., Parisi, G., & Aquiloni, L. 2010. Visual recognition of conspecifics in the American lobster, *Homarus americanus*. *Animal Behaviour*, **80**, 713-719.

Glinski, T. H., & Krekorian, C. N. 1985. Individual recognition in free-living adult male desert iguanas, Dipsosaurus dorsalis. *Journal of Herpetology*, **19**, 541-544.

Gronenberg, W., Ash, L. E., & Tibbetts, E. A. 2008. Correlation between facial pattern recognition and brain composition in paper wasps. *Brain Behavior and Evolution,* **7**, 1-14.

Hurst, J. L., Payne, C. E., Nevison, C. M., Marie, A. D., Humphries, R. E., Robertson, D. H. L., Cavoggioni, A., & Beynon, R. J. 2001. Individual recognition in mice mediated by major urinary proteins. *Nature,* **414**, 631-634.

Irvine, A. B. 1998. Individual recognition in wild bottlenose dolphins: a field test using playback experiments. *Animal Behaviour,* **57**, 41-50.

Kuebler, L. S., Kelber, C., & Kleineidam, C. J. 2010. Distinct antennal lobe phenotypes in the leaf-cutting ant (*Atta vollenweideri*). *The Journal of Comparative Neurology,* **518**, 352-365.

Mery, F., & Kawecki, T. J. 2004. An operating cost of learning in Drosophila melanogaster. *Animal Behaviour,* **68**, 589-598

Michener, C. D. 1969. Comparative social behavior of bees. *Annual Review of Entomology,* **14**, 299-342.

Michener, C. D. 1974. *The social behavior of the bees: a comparative study.* Cambridge:

Belknap Press.

Muller, J. K., Eggert, A. K. & Elsner, T. 2003. Nestmate recognition in burying

beetles: the "breeder's badge" as a cue used by females to distinguish their mates

from male intruders. *Behavioral Ecology,* **14**, 212-220.

Niven, J. E., & Laughlin, S. B. 2008. Energy limitation as a selective pressure on the

evolution of sensory systems. *Journal of Experimental Biology,* **211**, 1792-1804.

O'Donnell, S. 1996. Reproductive potential and division of labor in wasps: are queen and

worker behavior alternative strategies? *Ethology Ecology and Evolution,* **8**, 305-

308.

O'Donnell, S. 1998. Reproductive caste determination in eusocial wasps (Hymenoptera:

Vespidae). *Annual Review of Entomology,* **43**, 323-346.

Pfennig, D. W., Gamboa, G. J., Reeve, H. K., Reeve, J. S., & Ferguson, I. D. 1983.

The mechanism of nestmate discrimination in social wasps (Polistes,

Hymenoptera: Vespidae). *Behavioral Ecology and Sociobiology,* **13**, 299-305.

Rautio, S. A., Bura, E. A., Berven, K. A., & Gamboa, G. J. 1991. Kin recognition in

wood frog tadpoles (*Rana sylvatica*) - factors affecting spatial proximity to

siblings. *Canadian Journal of Zoology-Revue Canadienne De Zoologie, 69*, 2569-2571.

Reeve, H. K. 1989. The evolution of conspecific acceptance thresholds. *American Naturalist, 133*, 407-435.

Reeve, H. K. 1991. Polistes. In: *The social biology of wasps* (Ed. by K. G. Ross & R. S. Matthews), pp. 99-148. Ithaca, New York: Comstock.

Reeve, H. K., Peters, J. M., Nonacs, P., & Starks, P. T. 1998. Dispersal of first "workers" in social wasps: Causes and implications of an alternative reproductive strategy. *Proceedings of the National Academy of Sciences, 95*, 13737-13742.

Schell, A., Rieck, K., Schell, K., Hammerschmidt, K., & Fischer, J. 2011. Adult but not juvenile Barbary macaques spontaneously recognize group members from pictures. *Animal Cognition, 14*, 503-509.

Sheehan, M. & Tibbetts, E. A. 2008. Robust long-term social memories in a paper wasp. *Current Biology, 18*, 851-852.

Sheehan, M. J., & Tibbetts, E. A. 2009. Evolution of identity signals: frequency‐dependent benefits of distinctive phenotypes used for individual recognition. *Evolution, 63*, 3106-3113.

Sheehan, M. & Tibbetts, E. A. 2010. Selection for individual recognition and the evolution of polymorphic identity signals in *Polistes* paper wasps. *Evolutionary Biology, 23*, 570-577.

Sheehan, M. & Tibbetts, E. A. 2011. Specialized face learning is associated with individual recognition in paper wasps. *Science, 334*, 1272-1275.

Sherman, P. W., Reeve, H. K., & Pfennig, D. W. 1997. Recognition systems. In: *Behavioral ecology: an evolutionary approach* (Ed. by J. R. Krebs & N. B. Davies), pp. 69-96. Oxford: Blackwell Scientific.

Sugita, Y. 2007. Face perception in monkeys reared with no exposure to faces. *Proceedings of the National Academy of Sciences, 105*, 394-398.

Sumner, S., Lucas, E., Barker, J., & Isaac, N. 2007. Radio-tagging technology reveals extreme nest-drifting behavior in a eusocial insect. *Current Biology, 17*, 140-145.

Tibbetts, E. A. 2002. Visual signals of individual identity in the wasp *Polistes fuscatus. Philosophical Transactions of the Royal Society B, 269*, 1423-1428.

Tibbetts, E. A. 2004. Complex social behaviour can select for variability in visual features: a case study in Polistes wasps. *Proceedings of the Royal Society of London. Series B: Biological Sciences,* **271**, 1955-1960.

Tibbetts, E. A. & Dale, J. 2007. Individual recognition: it's good to be different. *Trends in Ecology and Evolution,* **22**, 529-537.

Tibbetts, E. A. & Sheehan, M. J. 2013. In press. Individual recognition and the evolution of learning and memory in *Polistes* paper wasps. In: *Handbook of Invertebrate Learning and Memory*.

Trivers, R. L. 1971. The evolution of reciprocal altruism. *Quarterly Review of Biology,* **46**, 35-57.

West -Eberhard, M. J. 1969. The social biology of polistine wasps. *Miscellaneous Publications Museum of Zoology University of Michigan,* **140**, 1-101.