

design of online health communities, where the structure of social relations can be explicitly determined on the basis of individuals' health characteristics.

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Supporting Online Material

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Specialized Face Learning Is Associated with Individual Recognition in Paper Wasps

Michael J. Sheehan* and Elizabeth A. Tibbetts

We demonstrate that the evolution of facial recognition in wasps is associated with specialized face-learning abilities. *Polistes fuscatus* can differentiate among normal wasp face images more rapidly and accurately than nonface images or manipulated faces. A close relative lacking facial recognition, *Polistes metricus*, however, lacks specialized face learning. Similar specializations for face learning are found in primates and other mammals, although *P. fuscatus* represents an independent evolution of specialization. Convergence toward face specialization in distant taxa as well as divergence among closely related taxa with different recognition behavior suggests that specialized cognition is surprisingly labile and may be adaptively shaped by species-specific selective pressures such as face recognition.

The cognitive mechanisms underlying learning abilities are surprisingly similar across taxa as diverse as mammals, birds, insects, and mollusks (1). Although the mechanisms that underlie learning are broadly generalized across animals, there is increasing evidence that learning abilities are adaptively shaped by species' ecology and can be highly specialized (2). One of the most striking examples of specialized cognition is specialized face learning found in some mammals, including humans (3–5). Individual face recognition is an important aspect of human social

interactions, and our brains process the images of normal conspecific faces differently than any other images (6). Further, individual recognition is a type of complex social behavior that could favor specialized cognition (7) because it requires flexible learning and memory and has the potential to dramatically increase cognitive demands. However, the claim that face specialization is an adaptation to facilitate individual recognition has been contentious, in part because it is unclear whether face learning is based on conserved mechanisms or has evolved independently in multiple mammalian lineages (8, 9). If face specialization is an adaptation to facilitate face recognition, we predict that specialization will be associated with the evolution of facial individual recognition across distant taxa.

Paper wasps are a good system for examining the evolution of face specialization because closely related wasp species differ in their ability to individually recognize conspecific faces. The paper wasp, *Polistes fuscatus*, has variable facial features that are used to recognize individual conspecifics (10, 11). Visual recognition is possible in *Polistes* wasps because they have acute vision (12) and live in well-lit nests. *P. fuscatus* nests are often initiated by groups of cooperating queens, in which relative reproduction is determined by a strict linear dominance hierarchy (13, 14); individual recognition stabilizes social interactions and reduces aggression within these cooperative groups (15). Some wasp species, such as *Polistes metricus*, typically nest alone (16) and therefore lack competition among queens. Solitary nest founding is associated with a lack of facial pattern variability (17), and experiments have shown that *P. metricus* does not recognize conspecifics as individuals (18).

We tested the adaptive evolution of specialized face learning by comparing face specialization in *P. fuscatus* and *P. metricus*. We predicted that *P. fuscatus* will learn normal face images faster and more accurately than nonface images or manipulated faces (Fig. 1), whereas *P. metricus* will not. Comparing learning of normal and manipulated face images (Fig. 1) provides a particularly good test of face specialization because manipulated faces are composed of the same colors and patterns as those of normal faces (table S1), but alteration may prevent the perceptual system from identifying the stimuli as faces. We tested learning by training wasps to discriminate between two images using a negatively reinforced

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T-maze (fig. S1) (19). The floor of the entire maze was electrified, except for a “safety zone” in one arm of the maze, which was consistently associated with one image in a pair. The position of the safety zone switched across trials in a predetermined pseudo-random order. Wasps were placed in an antechamber, allowed to acclimate, and then released into the electrified maze for 2 min. A wasp “chose” when it entered a chamber in one of the arms of the maze. Each wasp was a healthy wild-caught adult female naïve to the training paradigm and was tested only once. We trained 12 wasps for 40 consecutive trials on each image type (Fig. 1). We compared the speed of acquisition using generalized estimating equations (GEEs) and total number of correct choices between image treatments using 2-by-2 χ^2 tests.

We found that individual recognition is associated with specialization for conspecific face learning in paper wasps. *P. fuscatus* distinguished

pairs of normal faces more rapidly and accurately than nonface and manipulated face images (GEE, full model: Wald $\chi^2 = 32.06$, $df = 4$, $P < 0.0001$, $n = 2400$ trials) (Fig. 2, A and B). These results are surprising because Hymenopteran visual systems are predicted to distinguish between high-contrast patterns more readily than complex images of natural scenes, such as faces and caterpillars (20). Nevertheless, *P. fuscatus* that were trained to discriminate faces learned faster (for trials 1 to 30: GEE, Wald $\chi^2 = 5.61$, $P = 0.018$, $n = 720$ trials) and made more correct choices than did wasps trained to discriminate simple patterns ($\chi^2 = 9.1$, $P = 0.0026$, $n = 960$ trials) (Fig. 3A). A greater familiarity with faces than patterns cannot explain the result because paper wasps are generalist visual predators of caterpillars (21) yet learn to discriminate between pairs of caterpillars more slowly (GEE, Wald $\chi^2 = 25.45$, $P < 0.0001$, $n = 960$ trials) and with fewer correct choices than

between pairs of faces ($\chi^2 = 45.02$, $P < 0.0001$, $n = 960$ trials) (Fig. 3A). The most striking evidence for specialized face learning in *P. fuscatus* is that they have trouble learning faces without antennae. Wasps learn pairs of antenna-less faces more slowly and less accurately than normal faces (lower rate of acquisition GEE, Wald $\chi^2 = 13.98$, $P < 0.0001$, $n = 960$ trials; and fewer correct choices $\chi^2 = 18.85$, $P < 0.0001$, $n = 960$ trials). Therefore, antennae are an essential cue for effective face recognition. In a separate image manipulation, we rearranged the components of the wasp face and found that facial configuration also influences learning. Wasps trained to discriminate pairs of rearranged faces had lower rates of acquisition (GEE, Wald $\chi^2 = 20.18$, $P < 0.0001$, $n = 960$ trials) and made fewer correct choices ($\chi^2 = 18.28$, $P < 0.0001$, $n = 960$ trials) (Fig. 3A) than did wasps trained to discriminate pairs of normal faces. Taken together, these data suggest that *P. fuscatus* do not use general pattern- or shape-discrimination abilities to recognize conspecific faces. Instead, faces appear to be treated as unique visual inputs.

We next examined how face specialization co-varies with individual face recognition by testing learning in *P. metricus*, which lacks individual recognition (18). *P. metricus* showed no evidence of specialized face learning. In fact, wasps trained to discriminate pairs of face images performed no better than chance ($\chi^2 = 0.2$, $P = 0.65$, $n = 480$ trials) (Fig. 3B). In contrast to *P. fuscatus*, *P. metricus* had higher rates of acquisition when trained to discriminate patterns and caterpillars than conspecific faces (GEE full model: Wald $\chi^2 = 8.48$, $df = 2$, $P = 0.014$, $n = 1440$ trials; patterns: Wald $\chi^2 = 8.27$, $P = 0.004$, $n = 960$ trials; caterpillars: Wald $\chi^2 = 4.02$, $P = 0.045$, $n = 960$ trials) (Fig. 2C). Additionally, *P. metricus* choose the correct pattern and caterpillar images more often than the correct conspecific face image (pattern: $\chi^2 = 10.47$, $P = 0.0012$, $n = 960$ trials, caterpillar: $\chi^2 = 7.37$, $P = 0.0066$, $n = 960$ trials) (Fig. 3B).

To ensure that the difference in face-learning abilities between the two species is caused by cognitive differences rather than the particular

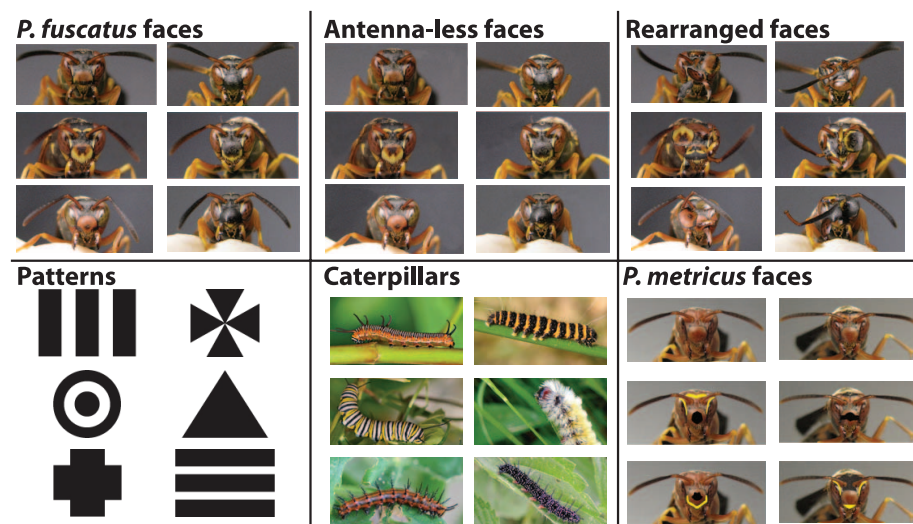


Fig. 1. Images used for training wasps. Wasps were trained to discriminate between pairs of images. Pairs are shown in the same row except for *P. metricus* face images. For *P. metricus* face images, the unmanipulated faces in the top row were paired with the manipulated images of the other face (for example, top left paired with middle left and bottom left). Image statistics for all images are provided in table S1.

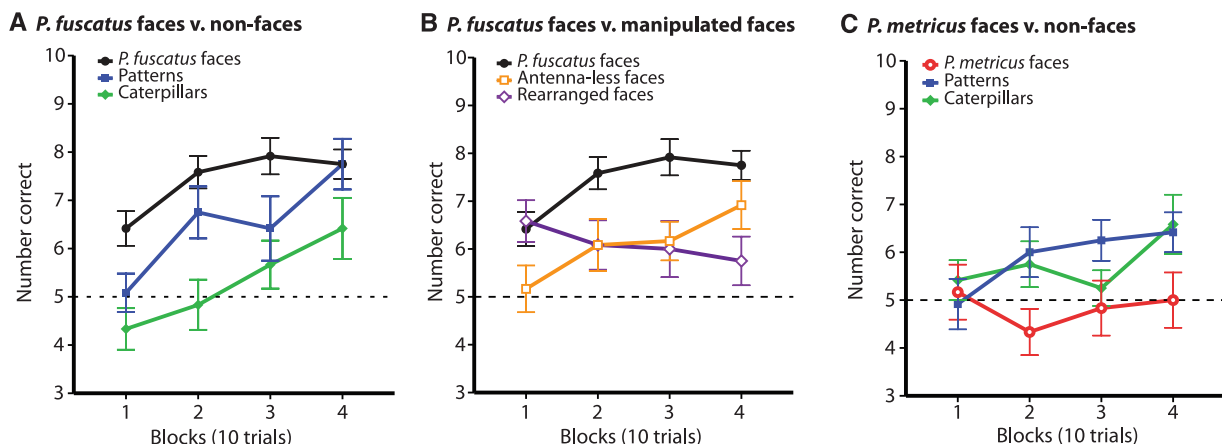


Fig. 2. *P. fuscatus* learned to discriminate between pairs of conspecific face images faster than (A) other images such as patterns and caterpillars and (B) manipulated face images. (C) *P. metricus* learned to discriminate between pairs of

patterns and caterpillars faster than conspecific face images. Line graphs show the mean number of correct choices (\pm SEM) per 10 trial blocks. Chance performance is 5 correct choices per 10 trial blocks; $n = 12$ wasps for each treatment.

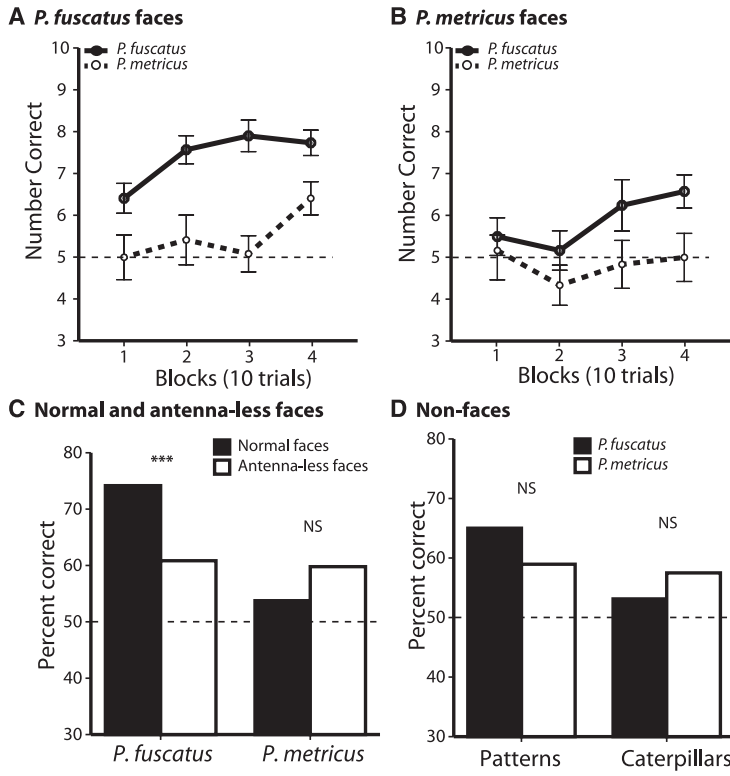
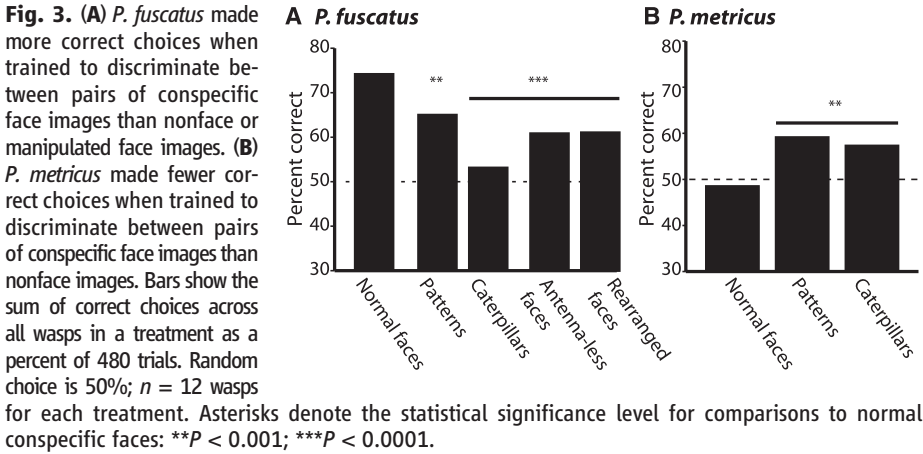


Fig. 4. *P. fuscatus* learned to discriminate between wasp face images faster than did *P. metricus* when trained to discriminate both (A) *P. fuscatus* and (B) *P. metricus* face images. Line graphs show the mean number of correct choices (\pm SEM) per 10 trial blocks. Chance performance is 5 correct choices per 10 trial blocks. (C) Removal of the antenna from faces decreases learning performance in *P. fuscatus* but not in *P. metricus*. (D) The two species make a similar percent of correct choices when learning nonface images. Bars show the sum of correct choices across all wasps in a treatment as a percent of 480 trials; $n = 12$ wasps for each treatment. Asterisks denote the statistical significance: NS, $P > 0.05$; *** $P < 0.0001$.

face stimuli used, we trained each species to discriminate heterospecific face images. *P. fuscatus* learned the face stimuli of both species more rapidly and made more correct choices than did *P. metricus* (rate of acquisition GEE full model: Wald $\chi^2 = 39.43$, $df = 2$, $P < 0.0001$, $n = 1920$ trials; *P. fuscatus* faces: Wald $\chi^2 = 32.38$, $P < 0.0001$, $n = 960$ trials; *P. metricus* faces: Wald $\chi^2 = 7.11$, $P = 0.008$, $n = 960$ trials; number correct choices, *P. fuscatus* faces: $\chi^2 = 42.52$, $P < 0.0001$, $n = 960$ trials; *P. metricus* faces: $\chi^2 =$

10.05, $P = 0.0015$, $n = 960$ trials) (Fig. 4, A and B). Although *P. metricus* learned face images poorly, they were able to discriminate between pairs of *P. fuscatus* faces; wasps performed better than chance in the last 10 trials (65.8%; $\chi^2 = 5.54$, $P = 0.019$, $n = 120$ trials) (Fig. 4A). We further analyzed whether *P. metricus* treat faces as unique visual inputs by examining how antennae removal influenced face learning. Unlike *P. fuscatus*, digital removal of the antennae from images did not reduce the number of correct

choices ($\chi^2 = 3.33$, $P = 0.068$, $n = 960$ trials) (Fig. 4C) or rates of learning (GEE, Wald $\chi^2 = 2.23$, $P = 0.14$, $n = 960$ trials), providing further evidence that faces are not special for *P. metricus*. Differences in face learning between the two species cannot be attributed to general differences in visual learning because both species learned to discriminate between pairs of artificial patterns and caterpillars at the same rate and with the same accuracy (rate of acquisition GEE full model: Wald $\chi^2 = 2.66$, $df = 2$, $P = 0.27$, $n = 1440$ trials; number correct choices patterns: $\chi^2 = 3.47$, $P = 0.063$, $n = 960$; caterpillars: $\chi^2 = 1.52$, $P = 0.22$, $n = 960$ trials) (Fig. 4D). Therefore, *P. fuscatus* and *P. metricus* differed only in their ability to learn normal face stimuli. Differences in visual acuity between the two species cannot account for the results because morphological measurements of facet diameter demonstrate that *P. metricus* is likely to have more acute vision than that of *P. fuscatus* (table S2 and fig. S2). Instead, specialized face learning is an evolutionarily labile trait that tracks individual recognition.

Overall, our data suggest that selection for efficient individual recognition has led to the adaptive evolution of specialized face learning in the paper wasp *P. fuscatus*. Specialized face learning provides a remarkable example of convergent evolution between wasps and mammals. Although mammals and wasps have dramatically different eyes and neural structures (22, 23), specializations for recognizing conspecific faces have arisen independently in both groups. Although specialized face learning in mammals and wasps are phenomenologically similar, they are likely to have different mechanistic bases. Face learning in primates and sheep is highly specialized, involving multiple brain regions and face-specific neurons (3, 24). Examining whether similar neural signatures of cognitive specialization are found in the “miniature” brain of an insect (25) provides an interesting avenue for future comparisons. The evolutionary flexibility of specialized face learning is striking and suggests that specialized cognition may be a widespread adaptation to facilitate complex behavioral tasks, such as individual recognition.

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financial interests. All data from these experiments are presented in the main text or supporting online material.

Supporting Online Material

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Materials and Methods
Figs. S1 and S2
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References (26–35)

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Modeling Effects of Environmental Change on Wolf Population Dynamics, Trait Evolution, and Life History

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Environmental change has been observed to generate simultaneous responses in population dynamics, life history, gene frequencies, and morphology in a number of species. But how common are such eco-evolutionary responses to environmental change likely to be? Are they inevitable, or do they require a specific type of change? Can we accurately predict eco-evolutionary responses? We address these questions using theory and data from the study of Yellowstone wolves. We show that environmental change is expected to generate eco-evolutionary change, that changes in the average environment will affect wolves to a greater extent than changes in how variable it is, and that accurate prediction of the consequences of environmental change will probably prove elusive.

Populations of the same species living in different environments often differ genetically or phenotypically. For example, the frequency of the genotype that determines whether a gray wolf (*Canis lupus*) has a black or gray coat varies with forest cover throughout North America (1). Similarly, wolves that predominantly feed on large prey are typically larger than those that specialize on smaller species (2). Numerous studies of a range of species also have reported that population dynamics and life history can vary across populations living in different environments (3, 4). In addition to these cross-population differences, environmental change within a population can generate rapid change in life history parameters such as generation length, in phenotypic trait and genotype distributions, and in population dynamics (5, 6). The eco-evolutionary consequences of environmental change are sometimes repeatable (7) but are frequently not (8). The wide range of population responses means that predicting likely dynamics has become one of the greatest challenges currently facing biology

(5). This is particularly true for species, such as the gray wolf, that play important roles in structuring ecosystems, because their response to environ-

mental change can have cascading effects across trophic levels (9). Given that environmental change can lead to potentially complex genetic, phenotypic, life history, and demographic responses, how can its likely consequences be explored? We show how integral projection models (IPMs) (10) provide a powerful framework to simultaneously investigate the ecological and evolutionary consequences of environmental change. We developed, applied, and analyzed one to explore how Yellowstone wolves may respond to environmental change.

Yellowstone National Park has experienced substantial environmental change in recent decades, with elk numbers declining, bison numbers increasing, and woody vegetation regenerating in some areas. These changes have been attributed variously to climate change, fluctuations in culling rates, and the reintroduction of wolves (11–14). Change is ongoing, with elk and bison numbers still trending in the same directions and further climate change being predicted (15). The

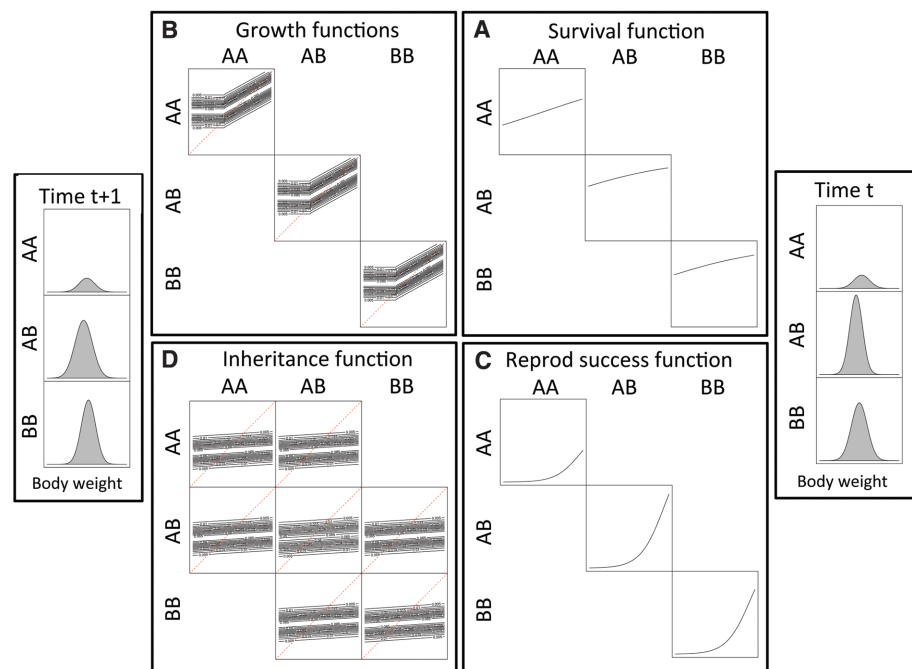


Fig. 1. (A to D) Graphical representation of the IPM that maps the bivariate distribution of genotype and body weight at time t to a new distribution at time $t + 1$. Functions (B) and (D) are probability density functions showing the range of y values for each x value; both of these functions are identical across genotypes. Associations between body weight and both survival and reproductive success varied with genotype, whereas growth rates and inheritance did not. Equations for these functions and parameter values can be found in tables S1 and S2. The body weight and genotype distributions at times t and $t + 1$ are, respectively, on the right and left of the functions to provide a graphical representation of the mathematical structure of the IPM (SOM).

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