SYMPOSIUM

A Morphological Integration Perspective on the Evolution of Dimorphism among Sexes and Social Insect Castes

Nicholas R. Friedman,[1,*] Vladimír Remeš[†] and Evan P. Economo[*]

*Biodiversity and Biocomplexity Unit, Okinawa Institute of Science and Technology Graduate University, 1919-1 Tancha, Onna, Okinawa Japan; [†]Department of Zoology & Laboratory of Ornithology, Faculty of Science, Palacký University, Tř. 17 Listopadu 50, Olomouc, Czech Republic

From the symposium "Multifunctional structures and multistructural functions: Functional coupling and integration in the evolution of biomechanical systems" presented at the annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2019 at Tampa, Florida.

[1]E-mail: nicholas.friedman@oist.jp

Synopsis Many species have evolved alternate phenotypes, thus enabling individuals to conditionally produce phenotypes that are favorable for reproductive success. Examples of this phenomenon include sexual dimorphism, alternative reproductive strategies, and social insect castes. While the evolutionary functions and developmental mechanisms of dimorphic phenotypes have been studied extensively, little attention has focused on the evolutionary covariance between each phenotype. We extend the conceptual framework and methods of morphological integration to hypothesize that dimorphic traits tend to be less integrated between sexes or social castes. In the case of social insects, we describe results from our recent study of an ant genus in which workers have major and minor worker castes that perform different behavioral repertoires in and around the nest. In the case of birds, we describe a new analysis of a family of songbirds that exhibits plumage coloration that can differ greatly between males and females, with apparently independent changes in each sex. Ant head shape, which is highly specialized in each worker caste, was weakly integrated between worker castes, whereas thorax shape, which is more monomorphic, was tightly integrated. Similarly, in birds, we found a negative association between dimorphism and the degree of integration between sexes. We also found that integration decreased in fairy wrens (*Malurus*) for many feather patches that evolved greater dichromatism. Together, this suggests that the process of evolving increased dimorphism results in a decrease in integration between sexes and social castes. We speculate that once a mechanism for dimorphism evolves, that mechanism can create independent variation in one sex or caste upon which selection may act.

Introduction

The differentiation of tissues to produce different forms despite a similar set of genetic instructions is a central theme in biology. Genetic similarity, as well as similarity in environmental cues, can lead to co-variation in the forms or traits that different tissues produce. This covariation between different traits, for example, between the shape of the ant eye and the ant mandible, is called morphological integration (Fig. 1A; Klingenberg 2008).

A significant body of literature has focused on the degree to which traits exhibit morphological integration and the processes by which selection leads traits to become more or less integrated (Olson and Miller 1958; Cheverud 1995; Goswami et al. 2014). Traits can covary when compared across individuals as a result of shared developmental mechanisms or functional coordination, and these processes also produce trait covariance when compared across many species (evolutionary integration; Cheverud 1996).

Here, we argue that the evolution of stable developmentally distinct phenotypes, dimorphism (and polymorphism; Simpson et al. 2011), can be thought of in a similar context. As with different traits in a single individual, the same trait in different individuals should exhibit some degree of morphological integration. Thus, the evolutionary covariation between worker and soldier ant morphology can be
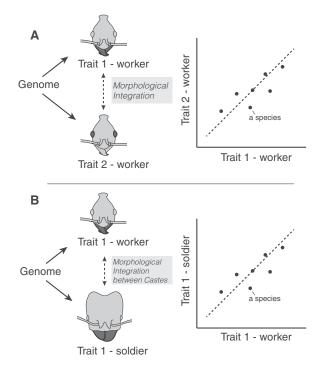
Fig. 1 Morphological integration between two traits produced by the same genome (**A**), using a hypothetical comparison between the minor worker's mandible and eye. Evolutionary covariation of the same trait between alternate phenotypes that are produced by the same genome can be seen as an extension of this concept (**B**). In this case, the hypothetical comparison is between the minor worker's mandible and the soldier's mandible.

considered a type of morphological integration (Fig. 1B), either as an extension of the concept or as a special case. To avoid confusion with other terms in the literature (many of which are reviewed in this issue by Farina et al. 2019; see also Cheverud 1996; Klingenberg 2008), we will refer to this morphological integration between dimorphic phenotypes as "integration between sexes/castes" throughout. In principle, if two traits are used for divergent functions, this process may occur in reverse and lead to a decrease in the covariation among traits (i.e., dissociation; Pie and Traniello 2007). We predict that the evolution of dimorphism should not only entail the gain of a difference between sexes or castes, but also a dissociation of their evolutionary trajectories.

Many types of dimorphism are commonly observed, including sexual dimorphism in many animal and plant species, caste or worker dimorphism in social insects (Wilson 1953; Hölldobler and Wilson 1990), and dimorphism in species that employ alternative reproductive tactics (Kodric-Brown 1986; Emlen 1997). Most studies of dimorphism focus on the difference between the phenotypes, and the process by which differential selection should lead to

this difference. In the context of sexual dimorphism, integration between sexes is often referred to synonymously with its assumed explanation, genetic correlation (Amundsen 2000). Integration between sexes is typically used as a null hypothesis in studies exploring the function of female ornaments (Amundsen 2000), and is seldom investigated as an end in itself. While many studies compare the extent of sexual dimorphism across species (Owens and Hartley 1998; Friedman and Remeš 2016 and references therein), the extent of covariation between dimorphic phenotypes has been left largely unexplored.

When genetic correlation and thus integration between sexes is strong, it may constrain the evolution of either sex from reaching its optimum, leading to sexual antagonism (Cox and Calsbeek 2009) and its equivalent in social insects, caste antagonism (Pennell et al. 2018). This evolutionary process can resolve itself (Cox and Calsbeek 2009) by an increase in dimorphism through a number of mechanisms (e.g., hormones Wheeler and Nijhout 1981, gene duplication Gallach and Betrán 2011). However, despite the evolution of sex differences, some degree of covariance should remain (Delph 2005). While studies of sexual and caste antagonism have explored the selective consequences of these processes within populations, many questions remain—particularly in extrapolating these processes to a deeper macroevolutionary time scale. In particular, some studies have predicted that integration should constrain the rate of trait evolution under some conditions (Wagner and Altenberg 1996), whereas others have found no such relationship (Goswami et al. 2014).

Here, we identify and attempt to address three questions regarding the evolution of dimorphism, all of which require or benefit from investigation in a phylogenetic context. First, are more dimorphic traits less strongly integrated between sexes and castes? While this may seem intuitive as integration must be relaxed to some degree, at some point in time, for a difference to have evolved in the first place, after the initial dimorphism evolves there could be any degree of integration. Traits that are different between sexes/castes may still evolve together. For example, soldier ants' heads could always be 15% larger than worker ants, and both change together in evolutionary time. Differences between soldiers and workers likely had already evolved before *Pheidole* began to diversify (as all species share worker dimorphism as a pleisiomorphic trait). Thus, dissociation is not necessary to maintain this difference, and it is not trivial to ask whether traits that are more different also tend to evolve more independently.

Several studies (Bonduriansky and Rowe 2005) and meta-analyses (Poissant et al. 2010) have found an indication of this reduction in integration between sexes in intraspecific comparisons. However, it remains unclear whether this pattern is retained when comparing variation among species (i.e., evolutionary integration) rather than among siblings. Second, are changes in the degree of dimorphism associated with changes in the degree of integration between sexes/castes? While this question is closely related to the first, addressing it requires a phylogenetic approach. Lastly, to what extent does the degree of dimorphism influence evolutionary rate? Traits that are not only evolving relatively independently in one sex or caste may be more labile/evolvable, but their rate could also depend on the type of selection involved. Below, we address these questions by comparing two systems that exhibit different types of dimorphism. We summarize relevant results from a recent study of worker caste dimorphism in ants, and compare them to a new study in birds that applies the same approach to sexual dimorphism in color.

Methods

Dimorphism and integration in social insect morphology

Ants are social insects that have evolved specialized morphologies for males, queens, often for workers, and occasionally different worker castes (reviewed in Wills et al. 2018). In a recent study, we examined evolutionary integration between the two dimorphic worker castes of the genus *Pheidole* (Friedman et al. 2019). In this genus, sterile workers develop into either minor worker (worker; Fig. 2A) or major worker (soldier; Fig. 2B) phenotypes, and their behavioral repertoire differs greatly depending on this morphological distinction (Wilson 1976a). Major workers exhibit a greatly enlarged head, with elongated posterior lobes that likely contribute to biting strength and a prominent anterior thorax (pronotum). In some species, major workers perform defensive roles in the colony (Wilson 1976b), whereas in others they spend more time milling seeds (Wilson 1984). Their developmental fate is determined by nutrition in a late stage of larval development, which when enriched triggers juvenile hormone and the development of a major worker (Rajakumar et al. 2018). Thus, major and minor workers can develop from the same genome through mechanisms that are understood and likely ancestral to the genus (Rajakumar et al. 2012).

Since major and minor workers perform different tasks in the colony, they likely have different optimal trait values for these tasks, causing differential selection that leads to dimorphism (Planqué et al. 2016; Pennell et al. 2018). This is an excellent system in which to examine morphological integration between worker castes because major workers exhibit specialized phenotypes beyond size differences, allowing us to test whether their phenotypes are evolving to become independent as well as different.

To test the hypothesis of a correlation between degree of integration and degree of dimorphism, we re-examine our recent analysis of *Pheidole* worker shape evolution (Friedman et al. 2019). We briefly describe here the methods used by Friedman et al. to quantify shape and infer evolutionary rates and integration, but further details can be found in the original study. To measure morphology of major and minor workers, we used a geometric morphometric approach to describe the major features of the head and thorax (in this article, we use the more familiar term "thorax," although in ants the thoracic segments are fused with the first abdominal segment, and this combined structure is often called the "mesosoma") in 214 species of *Pheidole* (sampling a mean of 2.2 major, 2.2 minor specimens per species). Using photographs in standard profile view (available on AntWeb, www.antweb.org), we placed 11 landmarks and 14 semi-landmarks on the head in the standard "full face view" and 6 landmarks on the thorax in "profile view" (Fig. 2B inset). On the head, semi-landmarks were reflected from the left side to the right, and fixed landmarks reflected and averaged across sides, to remove variation due to object symmetry. Landmarks for each specimen were aligned using a generalized Procrustes analysis in the R package *geomorph* 3.0.7 (Adams and Otárola-Castillo 2013). The set of landmarks from the head and thorax were treated as two different shape traits. We compared the evolutionary covariation between the major's head and the minor's head, and between the major's thorax and the minor's thorax, using a phylogenetically-corrected partial least squares analysis (Adams and Collyer 2016, 2018). This approach (Friedman et al. 2019) compared highly dimensional shape data in a phylogenetic context using a recent global phylogeny (Economo et al. 2019); and reported the correlation coefficient of the partial least squares regression (r-PLS) as a measure of integration. Significance was assessed using comparison to 1000 phylogenetically-transformed permutations of the morphological data. We estimated evolutionary rate using an approach also developed for highly dimensional shape data and implemented in *geomorph* (Adams 2014). In this approach, significance is assessed by comparison to rate
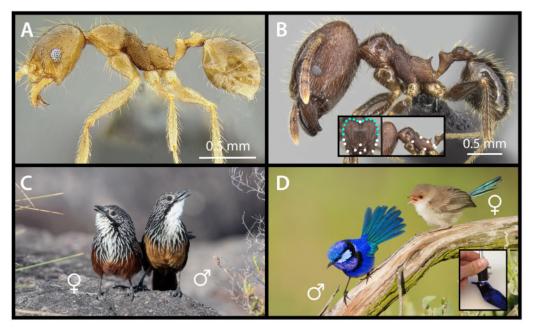
Fig. 2 Species in the ant genus *Pheidole* exhibit complete worker dimorphism. Birds in the genus *Amytornis* typically exhibit less sexual dichromatism than those in the genus *Malurus*. Standardized photos of *Pheidole fervens* minor worker (**A**) and major worker (**B**). Field photos of female and male White-throated Grasswren (**C**; *Amytornis woodwardi*; photo credit: Laurie Ross) and Splendid Fairy-wren (**D**; *Malurus splendens*; photo credit: Shelley Pearson).

ratios between traits from a null distribution of such ratios produced using a Brownian motion model of evolution (Denton and Adams 2015; Friedman et al. 2019). We re-examine the results of this analysis to test the hypothesis that the most dimorphic traits are also the least integrated.

Dimorphism and integration in feather coloration

One limitation of our study of worker caste dimorphism in ants is that complete dimorphism is ancestral to the genus of interest (*Pheidole*, sensu Wilson 1953; Rajakumar et al. 2012). Consequently, we were not able to test whether major changes in the degree of dimorphism were correlated with changes in the degree of integration between phenotypes, though this could be explored in future work with a broader phylogenetic scope. Furthermore, the results described earlier might be specific to either ants, social insects, or castes dimorphism and not applicable to other forms of dimorphism like sexual dimorphism. To address this issue, we designed a similar set of analyses to explore the evolution of sexual dimorphism in feather coloration among a clade of birds that differ in their degree of dimorphism.

The fairy-wrens and allies (*Maluridae*; Fig. 2C, D) are a family of Australasian songbirds that exhibit some of the most striking colors in the animal kingdom. The most spectacular of these belong to a single genus (*Malurus*; Fig. 2D). Within this group

sexual dimorphism in color (dichromatism) is common, and varies in degree among different parts of the body (Rowley and Russell 1998; Friedman and Remeš 2015). In contrast, the grasswrens (*Amytornis*) are a drab sister genus to the fairy-wrens and emu-wrens. Their plumage tends to be monochromatic and a close match to the visual background of their spinifex-dominated habitat (Rowley and Russell 1998; Friedman and Remeš 2015; Fig. 2C). Monochromatism is exhibited by most species in the group to which Malurids belong, the honeyeaters and allies (*Meliphagoidea*), and is most likely ancestral in *Maluridae* (Friedman and Remeš 2015; Friedman and Remeš 2017). Thus, contrasts between fairy-wrens and grasswrens should be indicative of derived changes in fairy-wrens.

We used data gathered as part of a previous study of sexual dichromatism in the fairy-wrens and allies (Friedman and Remeš 2015); color measurements are described in additional detail in that paper. In brief, we used reflectance spectrometry to measure coloration of museum specimens at the Australian National Wildlife Collection. We measured 11 plumage patches on females and males of 23 species in *Maluridae* (sampling a mean of 2.7 female, 3.6 male specimens per species). Color is a complex behavioral experience, and measurements have been designed to describe how it differs from one bird's feathers to another's (Montgomerie 2006). Unlike Friedman and Remeš (2015), we sought to compare

variation in plumage coloration without reducing it to individual axes of variation. To accomplish this, we used a visual model implemented in the R package *pavo* 2.0 to estimate relative receptor stimulation values for each reflectance spectrum using average avian violet-sensitive visual system (Vorobyev et al. 1998; Maia et al. 2018). As recommended by Maia et al. (2013), we reduced the axes of the tetrachromatic color space to a topology that is more appropriate for phylogenetic comparative methods using a principal components analysis (PCA).

To compare the evolution of plumage color between sexes and plumage patches, we used methods developed to estimate evolutionary rate and integration of highly dimensional characters like shape (Adams 2014; Adams and Collyer 2016). These are largely identical to methods described in the study of ants above, with the exception that here we applied them to matrices of continuous measures rather than to landmark coordinates. These analyses were performed using a phylogeny described by Lee et al. (2012). We estimated the degree of sexual dichromatism for each patch as the average Euclidean distance in color PCA space between males and females. We calculated evolutionary integration between sexes using a two-block r-PLS of each feather patch in the female versus the male (Adams and Collyer 2016). Lastly, we fit joint evolutionary rate models to our color PCA data for each feather patch in males and females (Adams 2014). To examine changes in the degree of integration between sexes following the evolution of dichromatism, we repeated the analyses described above separately for *Malurus* and *Amytornis*.

Results

Dimorphism and integration in social insect morphology

All possible comparisons between major and minor workers' head and thorax shape were significant as compared to a permutation of phylogenetically-transformed data (Adams and Collyer 2018). Among these, the strongest relationship was present in thorax shape as compared between major and minor workers (r-PLS = 0.76, $P = 0.002$; Fig. 3). The weakest relationship was observed in head shape as compared between major and minor workers (r-PLS = 0.48, $P < 0.001$). A contrast of these relationships using a z-test (implemented in the *compare.pls* function in *geomorph*) confirmed that the head exhibits a significantly lower degree of morphological integration between worker castes than the thorax ($P < 0.001$). Thus, evolutionary changes in the

minor's thorax should be more often accompanied by changes in the major's thorax than changes in the head.

Rates of shape evolution were roughly three times higher in the thorax compared to the head for both major and minor workers. Some difference in rate was expected due to a difference in the number of landmarks placed on each trait, and was corrected for by comparison against rate ratios of data simulated under these conditions (Denton and Adams 2015). Contrasts of rates of evolution between the head and thorax were significant for major workers (rate ratio = 1.65, $P < 0.01$) and for minor workers (rate ratio = 1.4, $P < 0.01$). Our results indicated that major workers evolved roughly 1.1 times more rapidly than minor workers, though this result was not significantly supported when compared to the simulated null distribution (Head$_{maj}$ vs. Head$_{min}$, rate ratio = 1.2, $P = 0.2$; Thorax$_{maj}$ vs. Thorax$_{min}$, rate ratio = 1.1, $P = 0.6$; Fig. 5A).

Dimorphism and integration in feather coloration

We found clear differences among plumage patches in their degree of evolutionary covariance in color between males and females, and these are described in a morphogram heat map (Fig. 4A; Martin and Wainwright 2011). Flight feathers (primaries, PR and tail feathers, TA) showed the greatest degree of integration between sexes, which was expected due their consistent flight function in both sexes (Burtt 1981). These patches were also the least dichromatic (Fig. 4B). The patches that exhibited the smallest degree of integration between sexes were the wing coverts (WI; Fig. 4A), cheek (CH), flank (FL), and belly (BE); these tend not to be ornamented in females even among colorful species (Johnson et al. 2013). When comparing the level of dichromatism in each of the 11 patches to the degree of integration between sexes, we found a negative but non-significant association ($F_{1, 9} = 3.35$, $P = 0.1$). We repeated the analyses described above independently for the dichromatic genus *Malurus* and the monochromatic dull clade *Amytornis*. This showed that the correlation coefficient between sexes was between 0.06 and 0.24 lower in the dichromatic clade than in the monochromatic clade (95% confidence interval, two-tailed paired Student's t-test; $P = 0.013$).

We estimated evolutionary rate for the color of each feather patch in females and males. Male feather color evolved on average three-fold more rapidly than female color (two-tailed paired Student's t-test, $P = 0.01$). Contrasts of the rate of color evolution between males and females (in comparison to
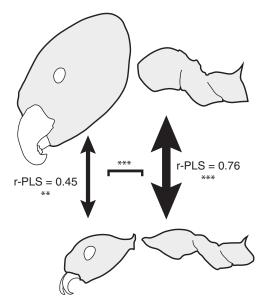
Fig. 3 Morphological integration between worker castes is weaker for head shape than thorax shape, as assessed via z-test. Phylogenetically controlled r-PLS coefficients are given along with their significance as assessed in comparison to a permutated null (Adams and Collyer 2018). *Source*: Adapted from Friedman et al. (2019).

simulated null; Denton and Adams 2015) rejected similar rates for six plumage patches: the belly, breast, flank, mantle, rump, and throat. Rates of evolution were positively correlated with the degree of dichromatism when compared among all 11 patches using ordinary least squares regression in both males ($F_{9,\ 1} = 5.6$, $P < 0.05$) and females ($F_{9,\ 1} = 7.1$, $P < 0.05$; Fig. 5B).

Discussion

In both studies we describe above, dimorphic traits exhibited a lower amount of integration; this observation applied to comparisons between both sexes and between social insect worker castes. In particular, we found that head shape, which is highly dimorphic in *Pheidole*, was less correlated between worker castes than relatively monomorphic thorax shape (Fig. 3). Likewise in birds, we found that more dichromatic feather patches tended to be less correlated between sexes, and that correlation was lower in the genus *Malurus* where dichromatism was derived (Fig. 4). We interpret these findings to suggest that the evolution of dimorphism not only increases the distance between dimorphic phenotypes in trait space, it also tends to decrease the degree of evolutionary integration between these phenotypes. These tests in a phylogenetic framework support previous observations obtained from comparisons of males and female phenotypes within
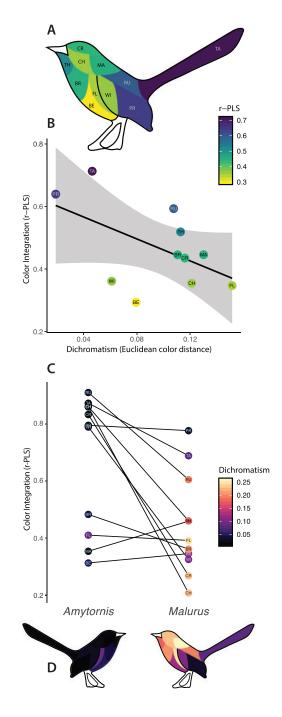

Fig. 4 Integration in color phenotype between sexes compared across 11 feather patches, with phylogenetically-corrected r-PLS coefficients expressed as a morphogram (A). More dimorphic feather patches tend to be less integrated between sexes (B). A transition to dichromatism in the genus *Malurus* (D) is associated with decreases in across-sex integration in many feather patches (C).

species that showed a negative relationship between dimorphism and integration between sexes (Poissant et al. 2010).
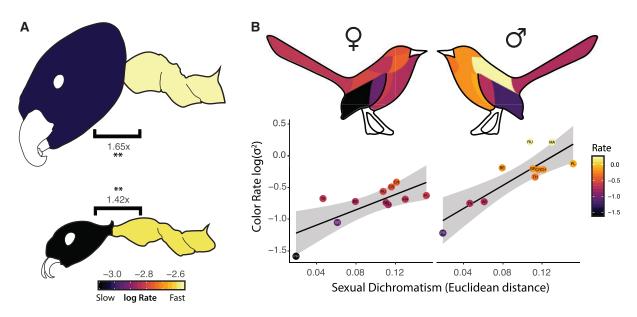
Fig. 5 Comparison of rates of evolution estimated for different traits in ants (**A**; *Pheidole*) and birds (**B**; Maluridae). Rate ratios are given in (**A**) in comparison to a simulated null, by which significance was assessed (see Denton and Adams 2015). Multivariate evolutionary rate estimates are shown in (**B**) for each feather patch and sex, and are compared to the degree of sexual dichromatism below. *Source*: Adapted from Friedman et al. (2019).

However, caution is due in accepting this result. While our contrasting integration between castes in *Pheidole* head shape versus body shape was based on an analysis of hundreds of species, the contrast itself is between only two traits. The more dimorphic trait was less integrated, but a sample of two other traits might yield a different pattern. Likewise, our regression of dimorphism and integration between sexes in birds was negative but not significant, which could reflect statistical power rather than the lack of an effect. Future studies that compare a larger number of traits, or use a more efficient statistical approach, are needed to definitively address this topic.

Integration and independence in social insect castes

The evolution of divergent worker morphologies is often seen as a hallmark of ants' social complexity, and much research has focused on the ultimate causes of worker dimorphism (Powell 2009; Planqué et al. 2016) and the investment of colony resources in each caste (McGlynn et al. 2012). Pie and Traniello (2007) compared morphological integration among *Pheidole* species within majors versus minors. Their results showed that worker morphology is less integrated in majors than in minor workers; our observations are similar despite using a different approach for measurement and analysis. This suggests that dimorphic traits like the posterior head of the major worker must dissociate not only

from the head of the minor worker, but also from the other traits that remain highly integrated between worker castes. Badyaev (2002) has described this as the necessity to "produce sexual dimorphism ... whilst maintaining the integrity of the developmental program."

Complete dimorphism is far from the rule in ant worker castes (Hölldobler and Wilson 1990). Indeed, Wilson (1953) described that workers often vary continuously between extreme phenotypes along a single allometric regression line (as in *Atta* leafcutter ants, whose majors are 5–7 times larger than the smallest workers). The divergent head shapes of many continuously varying worker castes suggests that they are under differential selection based on differing behavioral repertoires (Wilson 1980). Adaptation of extreme phenotypes toward conflicting optima despite a continuum of individual variation does not fit comfortably into the framework we have discussed in this article. Addressing integration between castes in these species continuously seems challenging, but a work-around for polyphasic species could be based on an approach like Via and Lande's (1985).

Proximate mechanisms

Investigating the proximate mechanisms of dimorphism is far beyond the scope of this article, however discussions of dimorphism tend to veer in this

direction and thus we feel an obligation to address proximate mechanisms to some extent. The proximate mechanism of evolving dimorphism should in general make expression of that trait conditional on some genetic or environmental cue. Often this is mediated by hormones, both in birds (Owens and Short 1995; Kimball and Ligon 1999) and in social insects (Wheeler and Nijhout 1981). Indeed, Ketterson et al. (2005) proposed that trait sensitivity to hormone concentration in one sex should predict independent trait evolution. However, the existence of bilateral gynandromorphs in birds and ants exhibiting characteristics of both sexes hints that some traits or proportion of their variation may be determined by genetic sex at the cellular level and not by hormonal control alone (Agate et al. 2003; Yang and Abouheif 2011).

Unless sex-linked, traits that are dimorphic should require one or many layers of modification that conditionally suppress or promote trait expression (Coyne et al. 2008). As these layers of modification accumulate and additively contribute to dimorphism in quantitative traits (see Badyaev 2002), we hypothesize that they should also reduce the extent to which dimorphic phenotypes covary. Each regulatory element should modify expression by some quantity to increase dimorphism. When this happens, intuitively this mechanism should introduce a degree of freedom, and locus upon which selection may act to affect one phenotype independently.

Rates of evolution

We found that rates of evolution were at least 1.5 times greater for thorax shape than for head shape in both major workers and minor workers, and greater than null expectations as assessed by simulation (Fig. 5A). Thus in social insects, the trait that was less dimorphic and more integrated between worker castes evolved more rapidly. We observed the opposite in our study of bird plumage: feather patches that were more dimorphic and less integrated between sexes tended to evolve more rapidly (Fig. 5B). If dimorphic traits are less integrated between sexes, this may remove constraints on the evolution of divergent phenotypes if one trait is experiencing stabilizing selection (Wagner and Altenberg 1996). For example, if female birds must be camouflaged to avoid predation while on the nest, changes in male phenotype should be limited if integration is strong and the female's optimum remains constant. However, Goswami et al. (2014) have shown that there is no correlation between morphological integration and evolutionary rate in

their examination of carnivoran crania. By comparing two different systems and finding conflicting results, we cannot support any general prediction of the effect of morphological integration on evolutionary rate.

Topics for future research

Alternative reproductive tactics that are associated with dimorphic phenotypes seem like an attractive system in which to study evolutionary integration and dimorphism. Indeed, many of the developmental mechanisms associated with caste determination in ants appear to be shared with strategy determination in other insects (Emlen et al. 2007; Rajakumar et al. 2018). For example, differential selection depending on these conditional strategies has led to divergent male phenotypes in dung beetles (Moczek and Emlen 2000). Large beetle larvae grow horns and compete for access to females as adults, whereas smaller larvae grow reduced horns and sneak past horned males by digging tunnels (Emlen 1997). If male dimorphism follows the same pattern that we describe above, we should expect that clades with greater dimorphism should exhibit decreased integration among horned and hornless phenotypes.

The system of worker caste dimorphism we describe above is a simplification of the complex caste structures observed in many social insects. In ants and termites, workers, soldiers, and reproductive males and females are all produced from the same genome (see Pennell et al. 2018). Many other organisms have life cycles whose alternating phenotypes must similarly be produced from the same genome (Sherratt et al. 2017). Indeed the sexual dichromatism described in fairy-wrens above is also a simplification: many males express dull plumage in early seasons that they spend helping to siblings on their natal territory (delayed plumage maturation; Karubian 2002), as well as "eclipse" plumage during the non-breeding season (Karubian et al. 2009). Research on sexual dimorphism has focused primarily on the difference between divergent phenotypes; this and other fields could benefit from examining each as a distinct trait.

Acknowledgments

SICB 2019 symposium on morphological integration provided stimulating questions and thoughtful discussion, as did M. Zelditch, A. Hund, M. Kawata, S. Chiba, and J. Urabe, and members of the Economo Unit.

References

Adams DC. 2014. Quantifying and comparing phylogenetic evolutionary rates for shape and other high-dimensional phenotypic data. Syst Biol 63:166–77.

Adams DC, Otárola-Castillo E. 2013. *geomorph*: an R package for the collection and analysis of geometric morphometric shape data. Methods Ecol Evol 4:393–9.

Adams DC, Collyer ML. 2016. On the comparison of the strength of morphological integration across morphometric datasets. Evolution 70:2623–31.

Adams DC, Collyer ML. 2018. Multivariate phylogenetic comparative methods: evaluations, comparisons, and recommendations. Syst Biol 67:14–31.

Agate RJ, Grisham W, Wade J, Mann S, Wingfield J, Schanen C, Palotie A, Arnold AP. 2003. Neural, not gonadal, origin of brain sex differences in a gynandromorphic finch. Proc Natl Acad Sci U S A 100:4873–8.

Amundsen T. 2000. Why are female birds ornamented? Trends Ecol Evol 15:149–55.

Badyaev AV. 2002. Growing apart: an ontogenetic perspective on the evolution of sexual size dimorphism. Trends Ecol Evol 17:369–78.

Bonduriansky R, Rowe L. 2005. Intralocus sexual conflict and the genetic architecture of sexually dimorphic traits in *Prochyliza xanthostoma* (Diptera: Piophilidae). Evolution 59:1965–75.

Burtt EH. 1981. The adaptiveness of animal colors. Bioscience 31:723–9.

Cheverud JM. 1995. Morphological integration in the Saddleback Tamarin (*Saguinus fuscicollis*) cranium. Am Nat 145:63–89.

Cheverud JM. 1996. Developmental integration and the evolution of pleiotropy. Am Zool 36:44–50.

Cox RM, Calsbeek R. 2009. Sexually antagonistic selection, sexual dimorphism, and the resolution of intralocus sexual conflict. Am Nat 173:176–87.

Coyne JA, Kay EH, Pruett-Jones S. 2008. The genetic basis of sexual dimorphism in birds. Evolution 62:214–19.

Delph LF. 2005. Processes that constrain and facilitate the evolution of sexual dimorphism. Am Nat 166:S1–4.

Denton JSS, Adams DC. 2015. A new phylogenetic test for comparing multiple high-dimensional evolutionary rates suggests interplay of evolutionary rates and modularity in lanternfishes (Myctophiformes; Myctophidae). Evolution 69:2425–40.

Economo EP, Huang JP, Fischer G, Sarnat EM, Janda M, Narula N, Guénard B, Longino J, Knowles LL. 2019. Evolution of the latitudinal diversity gradient in the hyperdiverse ant genus *Pheidole*. Glob Ecol Biogeogr 28:456–70.

Emlen DJ. 1997. Alternative reproductive tactics and male-dimorphism in the horned beetle *Onthophagus acuminatus* (Coleoptera: Scarabaeidae). Behav Ecol Sociobiol 41:335–41.

Emlen DJ, Lavine LC, Ewen-Campen B. 2007. On the origin and evolutionary diversification of beetle horns. Proc Natl Acad Sci U S A 104:8661–8.

Farina SC, Knope ML, Corn KA, Summers AP, Bemis WE. 2019. Functional coupling in the evolution of suction feeding and gill ventilation of sculpins (Perciformes: Cottoidei). Integr Comp Biol. doi:10.1093/icb/icz022.

Friedman NR, Remeš V. 2015. Rapid evolution of elaborate male coloration is driven by visual system in Australian fairy-wrens (Maluridae). J Evol Biol 28:2125–35.

Friedman NR, Remeš V. 2016. Global geographic patterns of sexual size dimorphism in birds: support for a latitudinal trend? Ecography 39:17–25.

Friedman NR, Remeš V. 2017. Ecogeographic gradients in plumage coloration among Australasian songbird clades. Glob Ecol Biogeogr 26:261–74.

Friedman NR, Bennett B, Fischer G, Sarnat EM, Economo EP. 2019. Macroevolutionary integration of phenotypes within and across ant worker castes. Preprint at https://www.biorxiv.org/content/10.1101/604470v1.

Gallach M, Betrán E. 2011. Intralocus sexual conflict resolved through gene duplication. Trends Ecol Evol 26:222–8.

Goswami A, Smaers JB, Soligo C, Polly PD. 2014. The macroevolutionary consequences of phenotypic integration: from development to deep time. Philos Trans R Soc Lond B Biol Sci 369:20130254.

Hölldobler B, Wilson EO. 1990. The ants. Cambridge (MA): Harvard University Press.

Johnson AE, Jordan Price J, Pruett-Jones S. 2013. Different modes of evolution in males and females generate dichromatism in fairy-wrens (Maluridae). Ecol Evol 3:3030–46.

Karubian J. 2002. Costs and benefits of variable breeding plumage in the Red-backed Fairy-wren. Evolution 56:1673–82.

Karubian J, Swaddle JP, Varian-Ramos CW, Webster MS. 2009. The relative importance of male tail length and nuptial plumage on social dominance and mate choice in the red-backed fairy-wren *Malurus melanocephalus*: evidence for the multiple receiver hypothesis. J Avian Biol 40:559–68.

Ketterson ED, Nolan V Jr, Sandell M. 2005. Testosterone in females: mediator of adaptive traits, constraint on sexual dimorphism, or both? Am Nat 166:S85–98.

Kimball RT, Ligon JD. 1999. Evolution of avian plumage dichromatism from a proximate perspective. Am Nat 154:182–93.

Klingenberg CP. 2008. Morphological integration and developmental modularity. Annu Rev Ecol Evol Syst 39:115–32.

Kodric-Brown A. 1986. Satellites and sneakers: opportunistic male breeding tactics in pupfish (*Cyprinodon pecosensis*). Behav Ecol 19:425–32.

Lee JY, Joseph L, Edwards SV. 2012. A species tree for the Australo-Papuan Fairy-wrens and allies (Aves: *Maluridae*). Syst Biol 61:253–71.

Maia R, Rubenstein DR, Shawkey MD. 2013. Key ornamental innovations facilitate diversification in an avian radiation. Proc Natl Acad Sci U S A 110:10687–92.

Maia R, Gruson H, Endler JA, White TE. 2018. *pavo* 2.0: new tools for the spectral and spatial analysis of colour in R. bioRxiv (doi.org/10.1101/427658)

Martin CH, Wainwright PC. 2011. Trophic novelty is linked to exceptional rates of morphological diversification in two adaptive radiations of *Cyprinodon* pupfish. Evolution 65:2197–212.

McGlynn TP, Diamond SE, Dunn RR. 2012. Tradeoffs in the evolution of caste and body size in the hyperdiverse ant genus *Pheidole*. PLoS One 7:1–5.

Moczek AP, Emlen DJ. 2000. Male horn dimorphism in the scarab beetle, *Onthophagus taurus*: do alternative reproductive tactics favour alternative phenotypes? Anim Behav 59:459–66.

Montgomerie R. 2006. Analyzing Colors. In: Hill GE, McGraw KJ, editors. Bird Coloration Vol. I: Mechanisms and Measurements. Cambridge, (MA): Harvard University Press. p. 90–147.

Olson EC, Miller RL. 1958. Morphological Integration. Chicago, USA: The University of Chicago Press.

Owens IPF, Hartley IR. 1998. Sexual dimorphism in birds: why are there so many different forms of dimorphism? Proc R Soc Lond B 265:397–407.

Owens IPF, Short RV. 1995. Hormonal basis of sexual dimorphism in birds: implications for new theories of sexual selection. Trends Ecol Evol 10:44–7.

Pennell TM, Holman L, Morrow EH, Field J. 2018. Building a new research framework for social evolution: intralocus caste antagonism. Biol Rev 93:1251–68.

Planqué R, Powell S, Franks NR, van den Berg JB. 2016. Disruptive selection as a driver of evolutionary branching and caste evolution in social insects. J Evol Biol 29:2111–28.

Pie MR, Traniello J. 2007. Morphological evolution in a hyperdiverse clade: the ant genus *Pheidole*. J Zool 271:99–109.

Poissant J, Wilson AJ, Coltman DW. 2010. Sex-specific genetic variance and the evolution of sexual dimorphism: a systematic review of cross-sex genetic correlations. Evolution 64:97–107.

Powell S. 2009. How ecology shapes caste evolution: linking resource use, morphology, performance and fitness in a superorganism. J Evol Biol 22:1004–13.

Rajakumar R, San Mauro D, Dijkstra MB, Huang MH, Wheeler DE, Hiou-Tim F, Khila A, Cournoyea M, Abouheif E. 2012. Ancestral developmental potential facilitates parallel evolution in ants. Science 335:79–82.

Rajakumar R, Koch S, Couture M, Favé MJ, Lillico-Ouachour A, Chen T, De Blasis G, Rajakumar A, Ouellette D, Abouheif E. 2018. Social regulation of a rudimentary organ generates complex worker-caste systems in ants. Nature 562:574–7.

Rowley I, Russel EM. 1997. Fairy-wrens and grasswrens Oxford, UK: Oxford University Press.

Sherratt E, Vidal-García M, Anstis M, Keogh JS. 2017. Adult frogs and tadpoles have different macroevolutionary patterns across the Australian continent. Nat Ecol Evol 1:1385–91.

Simpson SJ, Sword GA, Lo N. 2011. Polyphenism in insects. Curr Biol 21:R738–49.

Via S, Lande R. 1985. Genotype-environment interaction and the evolution of phenotypic plasticity. Evolution 39:505–22.

Vorobyev M, Osorio D, Bennett ATD, Marshall NJ, Cuthill IC. 1998. Tetrachromacy, oil droplets and bird plumage colours. J Comp Physiol A 183:621–33.

Wagner GP, Altenberg L. 1996. Perspective: complex adaptations and the evolution of evolvability. Evolution 50:967–76.

Wheeler DE, Nijhout HF. 1981. Soldier determination in ants: new role for juvenile hormone. Science 213:361–3.

Wills BD, Powell S, Rivera MD, Suarez AV. 2018. Correlates and consequences of worker polymorphism in ants. Annu Rev Entomol 63:575–98.

Wilson EO. 1953. The origin and evolution of polymorphism in ants. Q Rev Biol 28:136–56.

Wilson EO. 1976a. Behavioral discretization and the number of castes in an ant species. Behav Ecol Sociobiol 1:141–54.

Wilson EO. 1976b. The organization of colony defense in the ant *Pheidole dentata* Mayr (Hymenoptera: Formicidae). Behav Ecol Sociobiol 1:63–81.

Wilson EO. 1980. Caste and division of labor in Leaf-cutter Ants (Hymenoptera: Formicidae: *Atta*). Behav Ecol Sociobiol 7:157–65.

Wilson EO. 1984. The relation between caste ratios and division of labour in the ant genus *Pheidole* (Hymenoptera: Formicidae). Behav Ecol Sociobiol 16:89–98.

Yang AS, Abouheif E. 2011. Gynandromorphs as indicators of modularity and evolvability in ants. J Exp Zool Part B Mol Dev Evol 316:313–18.