

# Socially selected ornaments influence hormone titers of signalers and receivers

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Edited by Gene E. Robinson, University of Illinois at Urbana–Champaign, Urbana, IL, and approved June 10, 2016 (received for review February 17, 2016)

Decades of behavioral endocrinology research have shown that hormones and behavior have a bidirectional relationship; hormones both influence and respond to social behavior. In contrast, hormones are often thought to have a unidirectional relationship with ornaments. Hormones influence ornament development, but little empirical work has tested how ornaments influence hormones throughout life. Here, we experimentally alter a visual signal of fighting ability in *Polistes dominulus* paper wasps and measure the behavioral and hormonal consequences of signal alteration in signalers and receivers. We find wasps that signal inaccurately high fighting ability receive more aggression than controls and receiving aggression reduces juvenile hormone (JH) titers. As a result, immediately after contests, inaccurate signalers have lower JH titers than controls. Ornaments also directly influence rival JH titers. Three hours after contests, wasps who interacted with rivals signaling high fighting ability have higher JH titers than wasps who interacted with rivals signaling low fighting ability. Therefore, ornaments influence hormone titers of both signalers and receivers. We demonstrate that relationships between hormones and ornaments are flexible and bidirectional rather than static and unidirectional. Dynamic relationships among ornaments, behavior, and physiology may be an important, but overlooked factor in the evolution of honest communication.

honesty | challenge hypothesis | androgens | communication | social costs

The prevailing view in communication research is that hormones, such as androgens, influence the expression of ornaments and also function as “physiological costs” that maintain signal accuracy over evolutionary time (1). For example, the immunocompetence handicap hypothesis proposes that high androgen titers are required for animals to develop elaborate ornaments and high androgen titers also impose immune-related costs (2, 3). As a result, only the best individuals can afford to produce elaborate ornaments.

There is growing evidence that the unidirectional view of hormone/ornament relationships is incomplete (4, 5). Instead, relationships between hormones and ornaments may be bidirectional and therefore more complex than previously anticipated. Although there is little experimental evidence that ornaments influence hormone titers, theory suggests ornaments could affect the hormone titers of individuals displaying ornaments (signalers) and/or individuals perceiving ornaments (receivers) directly or indirectly via behavior.

Understanding how ornaments influence hormone titers of signalers and receivers is important because hormones have persistent effects on morphology, physiology, and behavior. Androgens in vertebrates and juvenile hormone (JH) in insects mediate the fecundity vs. lifespan tradeoff (6, 7). High titers of androgens and JH typically increase success in competitive contexts, but also decrease survival (8, 9). Therefore, if ornaments alter hormones, the hormonal changes will produce a cascade of subsequent effects on traits like social and sexual behavior, fertility, immunity, and survival. These phenotypic effects will influence how selection acts on ornaments (10, 11).

Ornaments may influence signaler hormones via indirect effects of ornaments on social behavior. Ornaments are well known to

influence social behavior (1). For example, agonistic ornaments influence the amount, intensity, and outcome of aggressive contests (12–14). Social behavior, in turn, influences hormone titers (15). For example, in many vertebrates, androgens increase during periods of social competition, increase in contest winners, and decrease in contest losers (16), although there is substantial variation in androgen response to social behavior across taxa and contexts (17, 18). In insects, JH responds to social stimuli in a way that parallels androgens in vertebrates (7, 19).

Experimental evidence that ornaments influencing signaler hormones is limited. Most notably, Safran et al. (5) showed that male and female barn swallows with artificially enhanced sexually selected ornaments have higher androgen titers than controls. This work provided the first evidence that ornament elaboration influences signaler physiology, although the factors that cause the physiological change remain untested. Other studies suggest that there may be complex interactions between ornaments and signaler physiology (11, 20), although controlled experimental analyses of how ornaments influence hormones and the mechanisms that underlie hormonal changes are lacking.

In addition to influencing signaler physiology, ornaments may also alter receiver physiology, although this possibility has not been tested. Ornaments convey information about their bearer’s overall “quality” such that individuals with elaborate ornaments constitute greater social and sexual threats than those with less elaborate ornaments (21). If individuals modulate hormone titers based on perceived threat, receivers may up-regulate androgens when rivals have elaborate ornaments but not when rivals have less elaborate ornaments. Although the effect of rival’s ornaments on hormones has not been tested, perceived threat influences social modulation of androgens (22). For example, Cichlid fish up-regulate androgens

## Significance

Despite the short-term benefits of dishonesty, animals typically communicate honestly. What prevents weak, low-quality individuals from cheating by signaling that they are strong? The general answer is that signals are costly, and only the best individuals can afford to signal strength. However, there are theoretical and empirical challenges associated with identifying the costs that maintain signal accuracy. Here, we provide a new perspective on honest communication by showing that wasps with dishonest signals are aggressively punished, and this punishment has lasting effects on the physiology of the dishonest signaler and those they interact with. We propose that interactions between behavioral and physiological costs of dishonesty could play an important role in maintaining honest communication over evolutionary time.

Author contributions: E.A.T. designed research; E.A.T. and K.C. performed research; Z.Y.H. contributed new reagents/analytic tools; E.A.T. analyzed data; and E.A.T., K.C., and Z.Y.H. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

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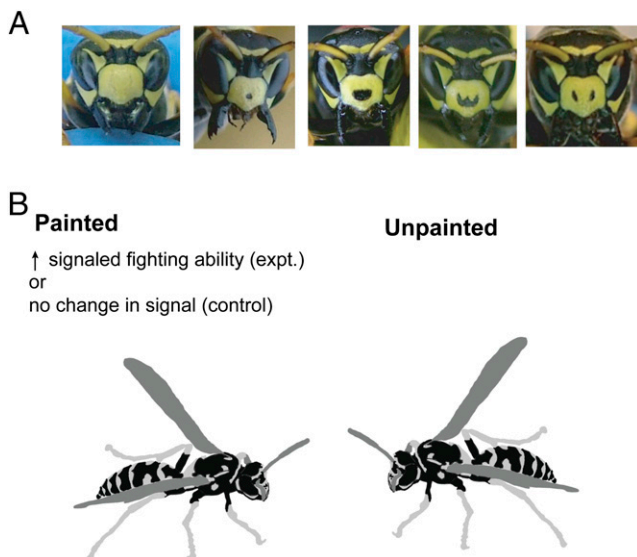
when a potential rival approaches their territorial boundary, but not when a known neighbor approaches the same boundary (23).

In this study, we provide the first experimental test, to our knowledge, of how ornaments influence the hormone titers of individuals with ornaments (signalers) and those they interact with (receivers), as well as the mechanisms that underlie hormonal changes. We experimentally altered a visual signal of fighting ability in *Polistes dominulus* paper wasps (Fig. 1A) and measured the behavioral and hormonal consequences of signal alteration. *P. dominulus* have variable black facial patterns that signal agonistic ability. Wasps with more broken black spots on their faces win more fights and are avoided by rivals compared with wasps with less broken black facial spots (24, 25). The hormone measured is JH, an invertebrate hormone that has strong functional parallels to androgens (7, 19). In paper wasps, JH is linked positively with dominance rank, aggression, and fertility (24, 26, 27) and negatively with survival (28). JH titers in *P. dominulus* are also socially responsive; JH increases during periods of social competition (29).

We tested how signals influenced social interactions and JH titers of signalers and receivers by setting up contests between pairs of unfamiliar wasps (Fig. 1B). The face of one wasp in each pair was painted to signal inaccurately high fighting ability (“bluffers,” experimental) or painted without altering their visual appearance (control). The other wasp in each pair remained unpainted. Wasps interacted for 2 h and then were bled for JH titer measurement. The short-term hormonal effects of interactions were measured in 65 pairs bled immediately, whereas the longer-term effects of interactions were measured in 28 pairs bled 3 h after the interaction.

## Methods

Nest-founding queens were collected from sites around Ann Arbor, MI, after they emerged from diapause. The early nest-founding period is a time of intense conflict because foundresses compete with many rivals before starting a nest (30). At collection, each wasp was weighed and photographed for analysis of natural facial patterns using established methods (24). Facial pattern analysis takes into account the number, size, and shape of black spots on the face. Wasps with higher facial pattern index have more broken



**Fig. 1.** (A) Portraits of five *Polistes dominulus* paper wasps, illustrating the variation in facial patterns that signal agonistic ability. (B) Illustration of experimental design. Two unfamiliar wasps compete. One wasp in each pair was painted so their facial patterns signal higher fighting ability (experimental) or painted without altering their visual appearance (control). The other wasp in each pair remained unpainted.

black spots on their face and signal higher fighting ability than wasps with lower facial pattern index (24, 31). Wasps were held in isolation in their nest with water and rock sugar for 2 d. Then, wasps were paired with a similarly sized rival (<5% difference by weight) for 2-h videotaped contests in 8- × 8- × 2-cm Plexiglas boxes. One wasp in each pair remained unaltered, whereas the other wasp was treated by painting its face (Fig. 1B). Rivals were collected from sites at least 5 km apart to ensure that they did not interact before behavioral trials.

The painted wasp received one of two treatments: either facial patterns were altered with paint so the wasp signaled a higher level of agonistic ability than the natural markings (experimental, inaccurate signaler) or natural facial patterns were painted without altering their appearance (paint control, accurate signaler). Paint control and experimental individuals received a similar amount of the same Testors enamel paint. However, the appearance of the experimental group was altered so that the facial patterns signaled that they were within the top quarter of the population, whereas the appearance of the paint control remained the same. This experimental design ensures that differences between experimental and paint control individuals were caused by changes in facial patterns rather than handling or use of paint. After painting, wasps were isolated for 5 min to allow paint to dry and then paired with an unpainted rival.

Pairs were allowed to compete in 2-h videotaped bouts. Later, aggression in bouts was scored by an observer blind to treatment and experimental predictions. Aggression levels were recorded as the number of mounts, bites, grapples, and stings, stereotyped aggressive behaviors found across the *Polistes* (32). The individual who initiated vs. received the aggression was recorded for mounts, bites, and stings. Both individuals are aggressive during a grapple, so both individuals were scored as initiating grapples. Grapples are rare (<2% aggressive acts).

After the behavioral trials, wasps were bled for analysis of JH titer. In 65 trials, wasps were bled immediately after the 2-h contests. In 28 trials, wasps were separated and housed in isolation for 3 h following the contest before being bled. The bleed times were chosen because previous work has shown that JH titers respond rapidly to the environment and the responses are maintained for 3 h (33, 34). JH measurement is fatal in small arthropods, so the JH of each wasp was measured one time. Wasps were assigned to treatment groups from a homogenous sample to ensure there were no consistent differences in individuals before experimental treatment. JH III titers in hemolymph were assessed using established radioimmunoassay methods developed by Huang and Robinson (35), and previously validated in *P. dominulus* (24).

Data were analyzed with general linear models in SPSS v. 22. The dependent variable was JH titer. The independent variables were natural facial pattern of self and rival, total aggression initiated, and total aggression received. The categorical independent variable was experimental treatment (paint control vs. experimentally altered face). JH titer, facial pattern, and aggression were  $\log(x + 1)$  transformed before analysis. Painted and unpainted wasps were analyzed separately because they are not statistically independent. The data were also split by bleed time, as patterns of JH responsiveness were different across wasps bled immediately and those bled 3 h after the trials. In sum, four discrete analyses were performed: bled immediately unpainted wasp; bled immediately painted wasp; bled 3 h later unpainted wasp; and bled 3 h later painted wasp.

## Results

**Behavioral Response to Inaccurate Signalers.** Wasps that signaled inaccurately high fighting ability (bluffers) suffered costly social interactions, in line with previous work in this system (36, 37). Bluffing increased the amount of aggression wasps received ( $F_{1,93} = 4.8$ ,  $P = 0.03$ ), but did not influence aggression initiated ( $F_{1,93} = 0.25$ ,  $P = 0.62$ ). Although unsurprising, this result is important because it shows that bluffers behave the same as wasps with accurate signals, although they are treated differently.

### Hormone Response to Inaccurate Signals: Immediate.

**Painted wasp.** Hormone titers were altered by inaccurate signaling. Immediately after contests, painted wasps with inaccurate signals had lower JH titers than controls with accurate signals (Table 1 and Fig. 2A). Bluffers had lower JH partially because they received more aggression than accurate signalers; JH was associated with the interaction between aggression received and natural facial patterns (Fig. 2B). The significant interaction suggests that receiving aggression decreased JH in wasps with natural faces that signal low

**Table 1. Results of a general linear model analyzing the factors associated with JH-titer in painted wasps immediately after contests**

Factor	F	P
Own signal accuracy (bluff vs. control)	9.51	0.003
Aggression received × own original facial patterns	7.46	0.01
Rival original facial patterns	0.71	0.40
Own original facial patterns	8.37	0.005
Aggression initiated	0.21	0.64
Aggression received	4.06	0.05

agonistic ability, but not in wasps with natural faces that signal high agonistic ability. To further explore the how a wasp's natural facial patterns influenced the relationship between JH titer and aggression, the data were split into wasps that signaled lower fighting ability (entirely yellow faces) and higher fighting ability (some black on face). Within wasps that signaled lower fighting ability, wasps that received more aggression had lower JH than wasps that received less aggression ( $F = 4.06$ ,  $r = 0.30$ ,  $P = 0.05$ ,  $n = 42$ ). Within wasps that signaled higher fighting ability, there was no relationship between aggression received and JH ( $F = 0.83$ ,  $r = 0.19$ ,  $P = 0.37$ ,  $n = 23$ ).

JH titer was also negatively linked with aggression received and positively linked with the wasp's own natural facial patterns but was not associated with rival facial patterns or aggression initiated (Table 1).

**Unpainted wasp.** JH titers of unpainted wasps were not linked with facial patterns or aggression initiated or received (signal accuracy of rival,  $F_{1,65} = 0.14$ ,  $P = 0.71$ ; own facial patterns,  $F_{1,65} = 0.16$ ,  $P = 0.69$ ; rival natural facial patterns,  $F_{1,65} = 0.54$ ,  $P = 0.46$ ; aggression initiated,  $F_{1,65} = 1.8$ ,  $P = 0.18$ ; aggression received,  $F_{1,65} = 0.01$ ,  $P = 0.94$ ).

#### Hormone Response to Inaccurate Signals: 3 h After Contest.

**Painted wasp.** Longer-term hormonal effects of ornaments were measured in a subset of wasps isolated for 3 h after contests and then bled for JH analysis. Painted wasps with inaccurate signals had significantly higher JH than controls with accurate signals (Table 2 and Fig. 2A), illustrating that signal inaccuracy has long-term effects on hormone titers. Surprisingly, signal inaccuracy has different effects on JH over the short and long term. Wasps

that fought rivals signaling high fighting ability had higher JH 3 h after contests than wasps that fought rivals signaling low fighting ability (Fig. 3A), suggesting that inaccurate signalers compensate for initial JH down-regulation.

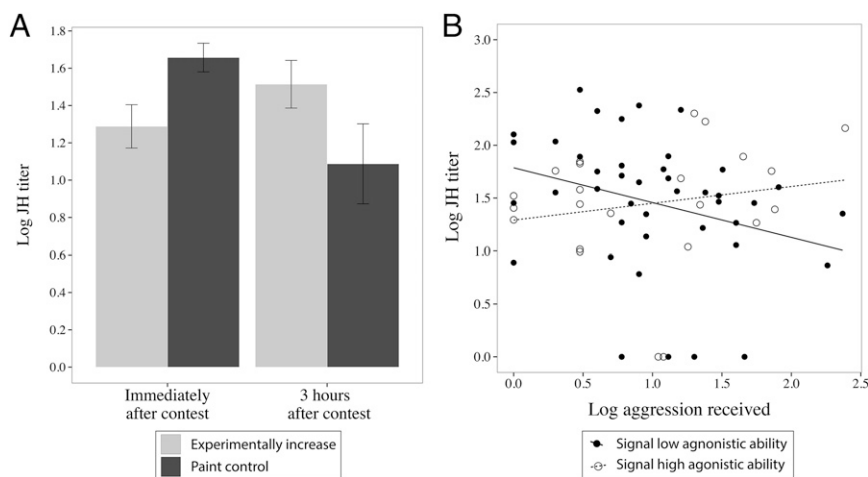
JH was also positively linked with rival facial patterns. Although wasps were randomly assigned rivals, wasps who fought rivals signaling high fighting ability had higher JH 3 h after contests than wasps who fought rivals signaling low fighting ability (Table 2 and Fig. 3A). In the full statistical model, JH was not linked with aggression initiated or received, although the signaler's natural facial patterns were positively linked with JH (Table 2).

**Unpainted wasp.** Among unpainted wasps, JH titers 3 h after the contest were influenced by rival signals. Wasps who fought rivals with natural facial patterns that signaled high agonistic ability had higher JH than those who fought rivals with natural facial patterns that signaled low agonistic ability (Table 3 and Fig. 3B). Rival signals themselves, rather than a correlate of the signals, caused the JH titers to change: wasps who fought bluffers had higher JH than wasps who fought rivals with unaltered faces (Fig. 3B). Other factors in the model were not significantly linked with JH, including aggression initiated and received and own facial pattern (Table 3).

#### Discussion

The results of this study challenge the prevailing view of hormone/ornament relationships by illustrating that ornaments influence the hormone titers of signalers and receivers. Signaler hormone titers are influenced indirectly via effects of ornaments on the social environment. Receiver hormone titers are influenced directly by rival ornaments. Hormones like JH and androgens have persistent effects on fitness (8, 9). Therefore, measuring the feedbacks among ornaments, physiology, and social behavior is essential to understand how selection acts on communication systems.

**Hormone Titers of Signalers.** Signal inaccuracy influenced the hormone titers of signalers. Wasps with inaccurate signals received more aggression than those with accurate signals and receiving aggression caused immediate JH suppression. Interestingly, the effect of aggression on JH titer varied with the wasp's natural facial patterns. Receiving aggression decreased JH in wasps with natural faces that signal low agonistic ability, but not in wasps with natural faces that signal high agonistic ability. Wasps often behave as if they "know" their own facial pattern (25). This study shows that the



**Fig. 2.** (A) Mean  $\pm$  SE Log JH-titer in wasps with accurate vs. inaccurate signals immediately and 3 h after contests ( $*P < 0.05$ ,  $**P < 0.005$ ). (B) Relationship between aggression received and JH-titer in painted wasps with natural facial patterns that signal low fighting ability (●) and high fighting ability (○) immediately following contests. For the figure, wasps categorized as low fighting ability had entirely yellow faces, whereas those categorized as high fighting ability had some black on the clypeus.

**Table 2. Results of a general linear model analyzing the factors associated with JH-titer in unpainted wasps 3 h after contests**

Factor	F	P
Rival signal accuracy (bluff vs. control)	6.83	0.016
Rival original facial patterns	9.05	0.006
Own original facial patterns	0.07	0.80
Aggression initiated	0.001	0.98
Aggression received	0.24	0.63

hormonal response to aggression varies based a wasp's perception of their own ability; receiving aggression causes JH down-regulation in weak wasps but not in strong wasps.

Surprisingly, the direction of the JH difference between accurate and inaccurate signalers was different over the short and long term (Fig. 2A). Wasps with inaccurate signals had lower JH titers than controls over the short term, but higher JH titers than controls over the longer term. This rapid change illustrates that JH titers respond quickly and flexibly to the social environment. Inaccurate signalers may be able to compensate for immediate JH down-regulation because they were isolated for the 3 h between contests and measurement of JH titer. In the wild, wasps experience more continuous social interactions (30), so JH down-regulation may be persistent.

The functional consequences of changing JH titers depend on the persistence of hormonal changes and frequency of social interactions. This study measured short-term changes in JH titers, so future work will be important to establish how long JH changes persist after social interactions. In the wild, even solitary *P. dominula* experience regular social interactions, because wasps compete with rivals over rank and nest ownership throughout the nest-founding period (38). When social interactions are common, even short-term changes in hormone titers could have substantial cumulative fitness effects. Future studies that measures JH response in additional time points and social contexts will provide broader understanding of how signal inaccuracy influences hormone titers across time and contexts.

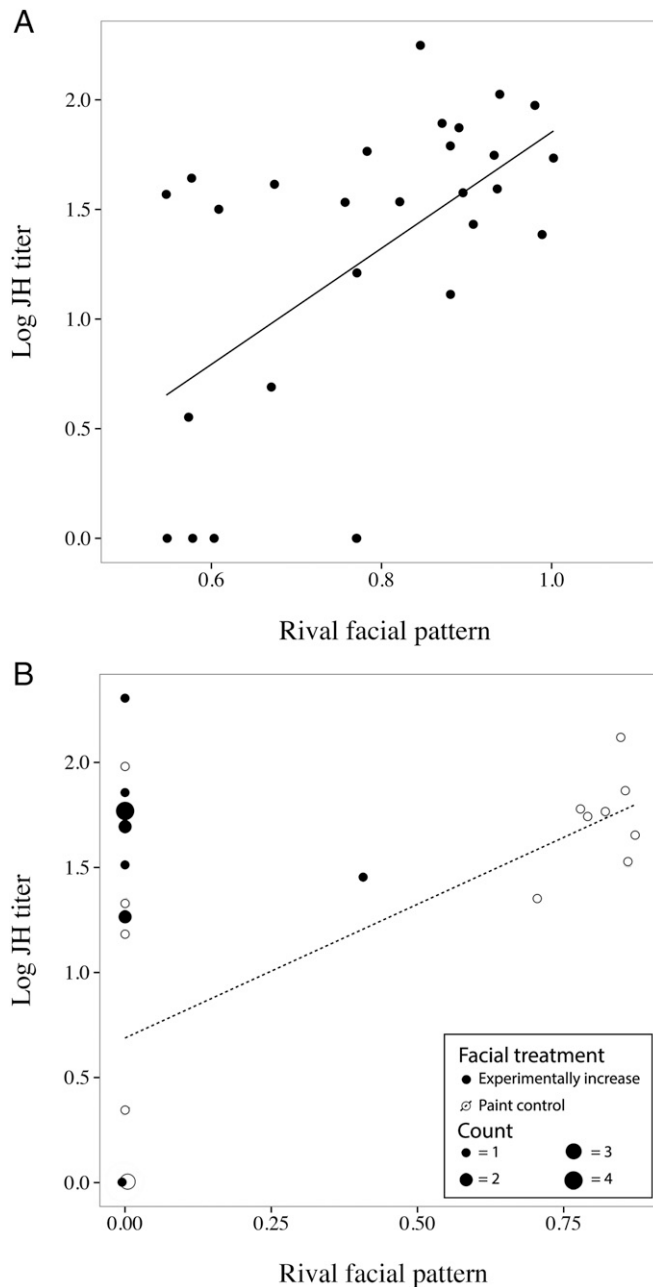
Why do accurate and inaccurate signalers have different JH titers? The experiment was designed to control extraneous factors, so divergence in JH titers between accurate and inaccurate signalers was caused by ornament inaccuracy influencing social interactions. Increased aggression received by inaccurate signalers is one key factor that reduced JH in bluffers (Fig. 2B), in line with other evidence that receiving aggression can cause hormone suppression (16). Subtle, nonaggressive aspects of social interactions could also contribute to the divergence of JH titers between accurate and inaccurate signalers, although these interactions are difficult to quantify.

**Hormone Titers of Receivers.** The effects of ornaments on physiology extend beyond the signaler: ornaments also directly influenced the JH titers of signal receivers. Wasps who interact with rivals signaling high agonistic ability had higher JH than those who interact with rivals signaling low agonistic ability, across both painted and unpainted wasps (Fig. 3). The positive relationship between rival ornaments and JH may occur if (i) rival ornaments directly influences JH titers or (ii) a correlate of rival ornaments, such as behavior, influences JH. We differentiated between these alternatives by measuring how experimentally altering signals influence rival JH titers. Wasps whose faces were experimentally altered to signal high agonistic ability caused JH up-regulation in rivals, whereas control wasps did. Therefore, JH is influenced by rival signals rather than a correlate of signals.

The effect of signals on rival JH is particularly interesting because facial patterns influenced receiver hormones directly, rather than working indirectly through behavior. Facial patterns

likely influence whether rivals are perceived as a threat (13), and this perception influences hormonal responsiveness. Perceived threat is known to influence hormonal response, although previous work has focused on factors such as ecology or social context rather than agonistic ability (39, 40).

Surprisingly, JH titers were more strongly linked with ornaments than aggression. Previous correlational and experimental studies have found links between JH and aggression in multiple insects, including *P. dominulus* (29, 41, 42). Although links between aggression and hormones are common (15), hormone/behavior links are context dependent and can easily be obscured by other factors (8, 18). In this study, who a wasp interacts with is more strongly linked with hormones than social behavior during



**Fig. 3.** Relationship between JH-titer and rival facial pattern 3 h after contests. (A) Rivals unpainted. (B) Rivals painted without altering their faces (○) and painted to experimentally increase signaled fighting ability (●).

**Table 3. Results of a general linear model analyzing the factors associated with JH-titer in painted wasps 3 h after contests**

Factor	F	p
Own signal accuracy (bluff vs. control)	5.66	0.026
Rival original facial patterns	6.44	0.019
Own original facial patterns	4.63	0.04
Aggression initiated	0.36	0.55
Aggression received	0.06	0.81

interactions. Relationships between ornaments and hormone titers are rarely tested, so future studies across additional taxa will be important to identify how ornaments influence the hormone titers of signalers and receivers.

**Overall Discussion.** What are the fitness consequences of changing hormone titers? Some integrative research that considers physiological costs has been critiqued for oversimplifying the costs and benefits of physiological processes. Hormones are unlikely to function as static “costs.” Instead, they are more like flexible “phenotypic integrators” (6) that change in response to the social environment and regulate expression of behavior, morphology, and physiology to match phenotype to the environment (6).

Despite the complexity of hormone/fitness links, even transient changes in hormones are likely to alter fitness via the persistent effect of hormones on morphology, physiology, and behavior. For example, in wasps, JH influences rank during early spring dominance contests (24, 26). Ranks are stable and determine lifetime reproductive opportunities (30). Therefore, JH down-regulation at the time of nest foundation may have long-term costs. In other taxa, transient down-regulation of hormones like androgens may have long-term fitness costs when there is a brief period of competition that shapes subsequent reproductive opportunities. For example, short-term androgen suppression during mating or territory establishment is likely to

have persistent effects on fitness. JH up-regulation may also influence fitness, as high JH reduces survival, with a particularly large survival effect on wasps that signal low agonistic ability (28). Therefore, ornament-induced hormonal changes are likely to have persistent fitness effects.

A key finding of this study is that there are links between social and physiological costs of ornamentation. Social cost models propose that a signaler’s interactions with receivers provide the cost that favors signal accuracy (43), whereas physiological cost models propose that production and maintenance of elaborate ornaments involve some type of physiological cost (e.g., metabolism, performance capacity, hormone titers) that favors accurate signaling (44, 45). We found paper wasps with inaccurate signals received more aggression than accurate signalers and receiving aggression caused rapid JH down-regulation. Therefore, inaccurate signaling produces a cascade of social and physiological effects.

Considering the links between social and physiological costs may resolve some challenges associated with studying these costs independently. For example, there are questions about whether receiving aggression is sufficiently costly to favor honest signaling (46). When social costs influence physiology, the consequences of social costs will persist after aggression ends, thereby broadening their impact. Physiological cost models assume links between signal elaboration and physiology, but it is often difficult to understand how these links are maintained. Social behavior could be the key intermediary in some systems (4, 11, 20).

In sum, the costly signaling literature will benefit from an integrative perspective that considers how different types of costs interact to influence ornament evolution. The dynamic interactions between hormones and ornaments may be an underappreciated factor in the evolution of honest communication systems.

**ACKNOWLEDGMENTS.** We thank Taylor Forrest, Allison Seltz, Ellery Wong, and Catherine Tait for assistance with behavioral observations. This material is based in part on work supported by National Science Foundation Grant IOS-1146139.

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