EFFECTS OF BODY SIZE ON EYE MORPHOLOGY AND VISUAL SIGNAL PRODUCTION IN SOCIAL WASPS

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ABSTRACT

Communication requires coordination between individuals producing signals and the individual acting on the information. While many studies have examined the evolution of signals and cognition, less work has explicitly considered the evolutionary consequences of signaling on sensory systems. First, in cases where sensory systems are already acute, signals enact little selective pressure. Alternatively, if sensory systems are relatively crude, sensory systems and the signals both may be elaborated in concert during the process of signal evolution. In this study we (1) tested these two scenarios by exploring visual signaling in *Polistes* paper wasps, and (2) predicted the potential for information transfer based on acuity and body size. We found that body size predicted eye morphology; however, presence of signaling did not. Furthermore, species of *Polistes* which signaled were not significantly different than non-signaling species. Lastly, *Polistes* were not significantly different than other genera. We, therefore, believe the visual system of *Polistes* was already sufficient to perceive signals when they appeared. We also found that the number of signals perceivable by the receiver may be constrained by the body size of the signaler. The influence of display area on potential for visual signaling may be a factor influencing evolution of visual communication in paper wasps. We believe that similar constraints may affect evolution of communication in other taxa.

INTRODUCTION

In its simplest form, communication occurs when information is transmitted from one individual (the sender) to another individual (the receiver). The receiver acquires information, processes it, and makes decisions based on the newly acquired knowledge (Endler 1993, Bradbury & Vehrencamp 1999, Seyfarth & Cheney 2003). Senders and receivers must be coordinated in order for information to be transferred effectively. Therefore, the evolution of signals depends on both the production of the signals, and responses from the receivers (Guilford & Dawkins 1991, Endler 1993, Wiley 2006).

Information transfer has three main steps: production, perception, and response. Signals must maximize information transfer to the receiver without large fitness costs to the sender. Studies have examined how selection creates signals that are efficiently produced and transmitted through the environment (Wiley & Richards 1978, Ryan & Brenowitz 1985, Gerhardt 1994, Leal & Fleishman 2004). The response of the receiver to the signal is required to maintain the signal in the population. A large body of research has been amassed about the response of receivers, typically through mate choice (Andersson 1982, Basolo 1990, Jang & Greenfield 1995). Despite the amount of research about signal production and receiver response, little research has examined how the evolution of sensory system may be influenced by signaling.

There are two hypothesis for how signaling may influence the evolution of sensory systems. (1) In many cases, sensory systems may show little evidence of evolution in response to communication. This may be because the sensory system evolved to facilitate other behaviors such as finding food or avoiding predators (Osorio & Vorobyev 1996, Endler & Basolo 1998, Christy *et al.* 2003, Herzner *et al.* 2005). If this was the case, the existing sensory system is sufficient to extract information from signals and there may be no selective pressure for the sensory system to evolve further (Mollon 1989). (2) Alternatively, it is possible that the ancestral state of the receiver had relatively crude sensory abilities for information transfer through signaling. In this scenario, we would expect selection to favor elaboration of the systems

to improve information transfer. Rather than signals evolving to capitalize on existing sensory systems, the signals and the systems would undergo correlated evolution (Fullard 1988, Desutter-Grandcolas 2002).

Sensory systems and signals are linked tightly together. Changes to the sensory system can alter information processing either by diminishing or increasing the ability to gain information from signals. Adaptive changes in sensory systems may be common in taxa which make use of novel signals. For example, most Lepidoptera lack auditory organs, but some moths that have evolved auditory structures to eavesdrop on bat echolocation have increased their ability to evade predators (Fullard 1988). The evolution of unique communication systems is intriguing because studying these cases explores how novel forms of communication arose. Through these studies, we can better understand the extent to which senders and receivers affect the evolution of communication systems.

Here, we will examine the evolution of visual communication in *Polistes* paper wasps. Visual communication in *Polistes* is of interest because apposition eyes are not ideal for viewing fine details such as small discrepancies between signals on other individuals (Snyder *et al.* 1977, Land & Nilsson 2002, Matthews & Matthews 2010). Highly acute vision would be necessary for the task and it may be costly if apposition eyes had to adapt for visual communication (Niven & Laughlin 2008). Furthermore, most insects tend to rely on chemical signals or vibrational signals to communicate (Hölldobler & Carlin 1987, Jackson & Mogan 1993, Virant-Doberlet & Cokl 2004, Cocroft & Rodriguez 2005). Indeed, in addition to visual signals, *Polistes,* like other social wasps, primarily communicate using chemical and vibrational signals (Dani *et al.* 1996, Dapporto *et al.* 2005). *Polistes* employ a visual communication system which suggests that they may have evolved a more acute sensory system than other social wasps.

Visual communication has evolved independently multiple times in *Polistes*. Communication occurs in two different forms. Quality signals reflect fighting ability and have evolved in at least two different lineages. Both *Polistes dominulus* and *Polistes exclamans* use quality signals (Pickett *et al.* 2006, Tibbetts & Lindsay 2008, Tibbetts & Sheehan 2011). Identity signals have evolved in *Polistes fuscatus*, which involve more complex, variable facial patterns on their clypeus and multiple parts of their body as a way of recognizing conspecifics (Sheehan & Tibbetts 2010). Following an interaction, individuals are able to remember each other for an extended amount of time; thus, also reducing conflicts (Sheehan & Tibbetts 2008). The multiple independent evolutions of two different signals make *Polistes* a good genus to study the effects of signaling on sensory system evolution. Through *Polistes*, we are able to compare the effects of signaling within the genus and also to other genera.

This study will focus on two topics: (1) assessing the factors that may influence visual acuity (measured by eye morphology), such as body size and presence of signaling, and (2) influence of acuity and body size on the potential for information transfer in the visual signals of social wasps.

We have several predictions for the evolution of signaling and visual acuity in *Polistes*. First, as with other insects, body size is expected to have a strong influence on eye morphology (Rutowski *et al.* 2008). Second, species with signals may have adaptations for perceiving differences in patterns among conspecifics. If this was true, species with signals should have morphological adaptations consistent with increased acuity. Alternatively, wasps with signals would have no morphological adaptations if the ancestral form of social wasps had sufficiently acute vision for visual communication. In addition to testing the role of signaling on sensory system evolution, we modeled the effects of visual acuity and signal production on information transfer in an effort to elucidate the effects of signal production and perception on the evolution of signaling in social wasps.

METHODS – MORPHOLOGY
Preserved Specimens
We measured body and eye morphology of females from 10 species of *Polistes* and 1 species of *Mischocyttarus*. Specimens had been preserved in a -20C freezer for 6 months to 4 years. Table 1 contains information on specimens. *Mischocyttarus* is a genus closely related to *Polistes* and has similar nesting behavior (Litte 1977, Arevalo *et al.* 2003). We also included published information for *Vespa crabro* and *Vespula vulgaris*, 2 species of hornets from a study by Kelber *et al.* (2011). *Vespa crabro* and *Vespula vulgaris* are more distantly related than *Mischocyttarus* to *Polistes* (Hines *et al.* 2006, Pickett &

Carpenter 2010). We compared *Mischocyttarus, V. crabro,* and *V. vulgaris* to *Polistes* to assess visual acuity in different genera. Greiner (2006) studied the eyes of *Apoica pallens* and *Polistes occidentalis* in detail, though we did not include the information because we measured different aspects of eye morphology.

Eye Measurements

A common way to study apposition eyes is to make replicas of the eye surface with clear nail lacquer (Grenier *et al.* 2004, Kelber *et al.* 2005). This can be done with preserved specimens without causing damage. The right eye of each individual was painted with a thin coat. We carefully removed the lacquer after allowing it to dry for a day and made small incisions at the dorsal, ventral, and either side of the eye using a scalpel (Fig. 1). The replica was then placed on a microscope slide and flattened with a coverslip. The flattened replicas were photographed at 45x magnification using a Wesco dissecting scope. We measured 2 factors of eye morphology from the photographs using Photoshop CS5: number of facets per eye and facet diameter.

In this paper, we examined a number of morphological predictors of visual acuity: facet number, maximum facet diameter and interommatidial angles ($\Delta\phi$). The number of facets in an eye determines resolution (Land 1997). A larger facet can capture more photons, increasing light sensitivity (Merry *et al.* 2005). Facet diameter was determined by measuring multiple areas using a grid-transect. Adobe Photoshop CS5 was used to overlay a grid comprised of 0.23 mm x0.23 mm (115 px x 115 px) squares on the eye replica image. The entire transect consisted of 20 points each located at 0.46 mm x 1.15 cm intervals. At each transect, measurements were taken of 5 facets by measuring the x, y, and z, axis of the hexagonal grid. The diameter of one facet of each transect point was found by averaging the three measurements. Then, the average facet size in each transect was found for each species. Finally, the max facet diameter was the largest facet from the transect averages.

The angle between the two ommatidia determines the resolving power of the local eye area (Barlow 1952). In general, larger facets have smaller $\Delta\phi$ (Land 1997, Merry *et al.* 2005, Rutowski 2008). Measurements of $\Delta\phi$ of from 3 live *P. fuscatus* were taken using methods presented by Rutowski and Warrant (2002). An opening just large enough for a wasp head was cut off of a 1 mL microcentrifuge tube. A single *P. fuscatus* was then placed inside the tube so the head was the exposed. The head was firmly secured using dental wax to disable all movement. Chalk dust was then lightly sprinkled over the right eye to serve as landmarks. The eyes were illuminated using two light sources on either side of the head to show the pseudopupils. We took measurements using the pseudopupil which appeared the darkest in the frontal ventral portion of the eye when the wasp was facing directly into the lens (Fig. 4). *P. fuscatus* have oval pseudopupils, stretched out dorsally and ventrally. This occurs because of a difference in $\Delta\phi$ in the x and y axis (Land 1993). The tube was secured to a Leitz goniometer in such a way that the wasp's head was centered on the platform and when rotated, the pseudopupils in both eyes would rotate symmetrically along the x, y, or z axes of the facets. A picture was taken each time the goniometer was rotated 10 degrees. This was repeated for the x, y, and z axes, which is critical because $\Delta\phi$ are not the same in each axis. Afterwards, in Adobe Photoshop, the number of facets the center of each pseudopupil moved was divided by the degrees moved to determine $\Delta\phi$. Table 2 contains eye morphology measurements.

The area of the eye with the largest facet diameter and smallest $\Delta\phi$ is called the acute zone. To visualize the acute zone in wasps, we mapped the distribution of facet diameters in *Polistes* and *Mischocytarrus*. We adapted a method used by Greiner (2006) to make eye maps. Images of eyes were fitted with colored circles of the widest diameter possible in Adobe Photoshop CS5. Each color corresponded with a specific facet diameter. The completed maps provided a visually informative way to compare the distribution of facets among different species (Fig. 2).

Body Measurements

We dissected wasps and measured the head, right hind leg, and right antenna of each individual. A Wesco dissecting scope at 45x magnification was used to view specimens. Images were captured using an Infinity 1 camera mounted on the dissecting scope. We used Infinity Analyze software to perform

measurements. We measured head width at the widest points of the head, dorsal to ventral eye height, hind femur length, and length of the first, long antenna flagellum segment (Fig. 1). Table 3 contains body measurement data.

Signaling Status

We separated *Polistes* into two groups: signaling and non-signaling species. Tibbetts (2004) described the variability of 69 species of *Polistes.* In this study, species with variable patterns on their clypeus were considered signaling species. *P. bahamensis* and *P. apachus* lack variable patterns and their clypeus and were considered non-signaling.

Statistics

We used a multivariate general linear model (GLM) to determine influence of signaling and body size on eye morphology in *Polistes.* A single *F* and p-value were reported because all tests (Pillai's Trace, Wilk's Lambda, Hotelling's Trace, and Roy's Largest Roots) provided identical statistical output. Linear regressions with individual confidence intervals were calculated for examining factors influencing eye morphology. Any data that fell outside the individual confidence intervals were considered significantly different. We performed several comparisons using principal component analysis (PCA) factor scores from femur and antenna length to body size compare with aspects of eye morphology. When finding the linear regression between genera, head size was used as a proxy for body size due to lack of femur length and antenna length data from *Vespa* and *Vespula*. Lastly, we calculated linear regressions for comparisons among eye height, facet number, and maximum facet diameter. We conducted all statistical analysis using PASW Statistics 17.

METHODS – VISUAL ACUITY MODEL

We modeled the potential for information transfer in wasps by considering the interaction of $\Delta\phi$, and clypeus size. Clypeus size provided a proxy for the area available for displaying visual signals. Across *Polistes*, variation in color pattern on the clypeus appears to be the most prominent means of signaling (Tibbetts 2004, Tibbetts & Sheehan 2010). The minimum size discrepancy between two patterns that the apposition eye can distinguish was calculated using the equation

$$x = \tan(\Delta\phi/2)*d*2 \qquad\qquad (1)$$

where x is the minimum perceivable size discrepancy, $\Delta\phi$ is in degrees, and d is the distance between the sender and the receiver (Fig. 2). The clypeus constrains the size of the signal that the sender can produce. Each signal must differ by the minimum size determined by $\Delta\phi$. Therefore, for a clypeus of size c, the number of possible signals, n, that can be seen by a wasp with an interommatidial angle of $\Delta\phi$, is

$$n = c/x \qquad\qquad (2)$$

Knowing both acuity and clypeus size can give an estimate of the necessary phenotypic differences that a species must possess to have usable signals. A surface graph of this equation was created in MATLAB.

We estimated the number of perceivable signal variants for each of our study species from this model. Using *P. fuscatus* with a known $\Delta\phi$, we estimated the $\Delta\phi$ of each species depending on the size of the maximum facet diameter. A change in ±1 µm of facet diameter from *P. fuscatus* corresponded to a ±0.05˚ and a ±0.10˚ change in acuity from 1.4˚. This created a range of estimated $\Delta\phi$ to calculate the number of perceptible signal variants. The estimated acuity was then paired with the species' average clypeus height to estimate the number of perceivable signals. *Vespa crabos* and *Vespula vulgaris* were excluded because clypeus measurements were unavailable.

RESULTS

Factors Influencing Eye Morphology

The results of the multivariate GLM are given in Table 4. The corrected model also showed that there was a strong correlation for eye height, facet number, and maximum facet diameter (eye height, $F_3 = 13.103$, p = 0.005, $r^2 = 0.801$; facet number $F_3 = 4.516$, p = 0.055, $r^2 = 0.540$, maximum facet diameter, $F_3 = 9.646$, p = 0.010, $r^2 = 0.742$). Body size, but not signaling predicts eye morphology in *Polistes*. It is significant for eye height, facet number, and maximum facet diameter (eye height, $F_1 = 22.680$, p = 0.003; facet number $F_1 = 5.491$, p = 0.058, maximum facet diameter, $F_1 = 15.137$, p = 0.008). Neither signaling nor the interaction between signaling and body size predicts eye morphology.

We directly examined the correlations between body size and eye morphology because multivariate models can often be difficult to interpret. Consistent with the multivariate approach, we found strong, positive correlations between body size and eye morphology in *Polistes* (Fig. 5). Larger wasps have greater eye height ($F_{1,8} = 43.032$, p = 0.001, $r^2 = 0.843$). The correlation between body size and facet number is strong ($F_{1,8} = 15.197$, p=0.005, $r^2 = 0.655$). Body size and maximum facet diameter also have a strong positive relationship ($F_{1,8} = 38.448$, p = 0.000, $r^2 = 0.828$).

Correlations between body size and eye morphology in *Polistes* are reflective of broader scaling trends across Vespid genera(Fig. 6). Head width is a significant and extremely strong predictor of eye height ($F_{1,2} = 264.690$, p = 0.004, $r^2 = 0.993$). It also has a strong relationship with maximum facet diameter ($F_{1,2} = 72.231$, p = 0.014, $r^2 = 0.973$). No regression calculation was performed between head size and facet number because the Kelber *et al.* (2011) study did not include data about the number of facets per eye.

Various eye morphology measurements show significant correlations when compared with each other in all our study species (Fig. 7). Eye height has a strong correlation with facet number and maximum facet diameter (facet number, $F_{1,9} = 56.989$, p < 0.001, $r^2 = 0.864$; maximum facet diameter, $F_{1,9} = 65.375$, p < 0.001, $r^2 = 0.856$). This suggests that an increase in eye size also leads to an increase in maximum facet diameter. Note that *M. mexicanus,* which has a small eye height, has the same maximum facet size as the larger *P. dorsalis* and *P. dominulus.* Facet number and maximum facet size have a positive relationship ($F_{1,9} = 9.349$, p = 0.014, $r^2 = 0.510$). Again, *M. mexicanus,* which is the smallest species with only 4805±200 facets per eye, has the same maximum facet diameter as *P. dorsalis* and *P. dominulus* which has more facets.

Modeling Information Transfer

Our model suggests that information transfer in social wasps is influenced more strongly by clypeus size than visual acuity (Fig. 8). The graph increases non-linearly as $\Delta\phi$ decreases because of the tangent function. However, within our estimated $\Delta\phi$ range for social wasps (1˚ - 2˚), the graph is essentially flat with respect to acuity. Thus, the minimum perceivable size discrepancy between two patterns changes relatively little across the span of $\Delta\phi$ we observed in social wasps. At a given acuity, the clypeus size has a greater effect on the potential for information transfer. The color gradient shifts are almost parallel to the $\Delta\phi$ axis. Therefore, within an $\Delta\phi$ range of 1˚ - 2˚, changes in $\Delta\phi$ has little effect on the number of perceivable signals. Instead, changes in clypeus size affect the number of signal variants the most. Signaling would be difficult with low visual acuity and small clypeus size. Figure 8b shows the graph from the side where the shape is easier to perceive. As distance drops from 1 cm to 0.5 cm, the color gradient becomes more perpendicular to the clypeus size axis (Fig. 8). Thus, increasing clypeus size has an even greater effect on perceivable signals. When distance increases from 1 cm to 2 cm, this effect is not as strong, but is still more influential than changes in $\Delta\phi$.

We fit the model with data from *P. fuscatus*. We found an average $\Delta\phi$ of 1.4˚ for *P. fuscatus*. At the theoretical distance of 1 cm, *P. fuscatus* can differentiate between patterns that differ by at least 0.244 mm. The average size of the clypeus of *P. fuscatus* is 1.79 x 1.73 mm (width x height). When clypeus height or width is used in equation 2, the number of perceivable signal variants is about 7 in for either horizontal or vertical directions. The number of differentiable signals in clypeus width for *P. fuscatus* is mapped on figure 8a.

To explore information transfer further in other Vespids, we fit the model with estimated $\Delta\phi$ from the other study species (Table 5). At a distance of 1 cm, we can see that species which have similar $\Delta\phi$, such as *M. mexicanus* and *P. dorsalis* have different numbers of perceivable signal variants. The only difference between the two species is that *P. dorsalis* has a larger clypeus and therefore allows more space for signal variation. Note that at a distance of 0.5 cm the amount of perceivable signals doubles, while viewing individuals at 2 cm away halves the amount of perceivable signals. However, the general pattern of the results is consistent.

DISCUSSION

We presented two scenarios of sensory system evolution in relation to signals. Sensory systems may be acute and signals evolve to capitalize on them for information transfer, or sensory systems and signals undergo correlated evolution to become more refined. Our results favor the former scenario, in which the evolution of novel signals has little impact on sensory evolution. Paper wasps species show variation in eye morphology, though the presence of visual signals is not predictive. Rather, body size is a strong predictor of differences in eye morphology among wasps. When we examined the effects of body size on eye morphology within *Polistes* and across genera, no species or genera show unique eye adaptations for signaling as we would expect if signals and vision had correlated evolution. Furthermore, we present a model that shows visual acuity has little influence on signal perception. Instead, it is the size of the signal display area which dictates the number of perceivable signals – this finding has greater implications towards future studies of communication.

Visual communication in *Polistes* is an ideal candidate for exploring the two scenarios of communication evolution. When we compared species within *Polistes,* species with signals do not have eye morphology that is significantly different from other non-signaling species; nor is the genus *Polistes* uniquely adapted for perceiving signals. This is surprising in some ways. Many insects have poor vision and cannot resolve images very clearly (Land 1993). Limited use of visual communication within a few select species in one genus of social wasps seems to predict that vision would become more acute with the advent of signals. However, wasps, like other flying insects, require acute eye sight for flight and capturing prey (Land 1993). The eye maps show that the acute zone of every eye is located in the frontal-ventral region of the eye (Fig. 2). Accordingly, this is where the largest facet diameters are and where many other studies have found the smallest $\Delta\phi$ in flying and predatory insects (Rossel 1979, Land & Eckert 1985, Rutowski & Warrant 2002, Merry *et al.* 2006). Selection for foraging and flight has likely favored acute vision that can be used for signaling. Furthermore, our model also shows that acuity would need to increase substantially for increased information benefits. Therefore, increasing acuity would cost more than the marginal fitness increase.

Our results show that body size is a strong predictor of eye morphology, adding to a large body of work on allometric scaling of body size and eye size in flying insects (Barlow 1952, Rutowski *et al.* 2008, Jander & Jander 2001). Body and eye sizes also scale positively across a range of other taxa including fish, reptiles, birds and mammals (Lyall 1957, Booke *et al.* 1999, Howland *et al.* 2004). Unsurprisingly, we also found that body size is positively correlated with eye morphology. This is expected, because larger wasps have larger heads, and consequently more space for eye development. Larger wasps also have greater maximum facet diameter, which correlates with smaller $\Delta\phi$. Thus, larger wasps have better vision in dimmer light and higher resolving power. Despite the large range of body sizes, wasps are all similarly acute relative to their body sizes. No species or genera had uniquely adapted eye morphology, which is consistent with the hypothesis that visual signaling in *Polistes* evolved to an already-acute sensory system.

The model we present shows that body size constrains the display area that can be used for signaling. Wasps with very acute vision (small $\Delta\phi$) and a large clypeus can perceive many signal variants, but highly acute wasps with a small clypeus will not perceive many signal variants. If the number of perceivable signals is too few, then the amount of information conveyed may be too small to favor

evolution of visual communication in the species. Therefore, body size may be a determining factor in the evolution of visual communication in Vespids.

Our model attempts to find the maximum amount of signal variation that can be perceived by a receiver. Many *Polistes* that signal do not use their entire clypeus for signaling. *P. dominulus* and *P. exclamans* have signals that are restricted to the center of their clypeus. The former uses signals in the form of various sized black dots that never exceed more than 39% of clypeus (Tibbetts & Dale 2004). Similarly, the signals of *P. exclamans* mostly vary in width, rather than height, and also do not completely cover the clypeus (Tibbetts & Sheehan 2011). The model we present likely overestimates perceivable signal variation because we were generous with our estimates of perceivable signals in different species of wasp. However, there is an even greater limitation posed by body size for small wasps if patterns do not span the entire clypeus. If *M. mexicanus* had signals, we calculated receivers could perceive a maximum of 3 possible signal variants in the vertical or horizontal directions. If the entire clypeus is not used like in other species, the actual number of perceivable would be even lower; signaling would be useless.

On the other hand, there are several caveats to our model. First, our model simplifies signal perception by looking at signal variation in only the vertical and horizontal directions. We assumed receivers analyze signals exclusively based on size. We cannot be sure that receivers pay attention to the size of the signal itself, or if they compare the area the signal occupies relative to the total area it is displayed upon. For example, take two individuals (A and B), each with a quality signal that is 0.5 mm^2. Individual A has a clypeus that has an area of 1 mm^2, while individual B has a clypeus that is 2 mm^2. If only the signal size is considered, these two individuals are of equal strength. If the signals are compared relatively to the clypeus, individual A has a signal which is 50% of the total display area, while individual B has a signal that only occupies 25% of the total area. In this case, individual A may be seen as more dominant. Signals are also variable in shape and color. The stripes of color which border the inner edges of the eye in *P. fuscatus* vary in width and height as it wraps around the contour of the eye. To make things more complicated, the eye stripe is also made of both a darker brown overlaid with a yellow stripe which varies in how high it reaches along the eye. A previous study by Tibbetts (2002) showed that receivers are paying attention to these signal changes, though operationalizing these signals for studies is much harder. In reality, wasps most likely pay attention to more factors (e.g. color intensity) than just the width and height differences in signals. Our model may still be a good fit for some wasps, such as *P. bellicosus* and *P. exclamans*, where signals vary only in vertical and horizontal sizes.

Visual communication in wasps is an area of particular interest, but how visual communication in these species evolved has not been well researched. Many Vespids lack variable facial patterns and therefore cannot signal. Three factors are likely to influence the distribution of visual signals in social wasps. First, the light environment can influence whether visual communication is useful. Many Vespid species live within enclosed nests, as in the case of hornets (Jeanne 1975). Due to low light conditions, individuals cannot use visual signals; these species continue to rely on chemical and vibrational signals. Other Vespid species do not build closed nests. Instead, the nest is a collection of open combs attached by a pedicle to a suitable nesting site (Ishay 1975). Visual signals have a greater chance of evolving in open faced nests because there is abundant light for viewing conspecifics. Indeed, we see that all *Polistes* have open faced nests, yet there are other genera with open nests that do not signal, such as *Mischocytarrus, Belonogaster, Parapolybia,* and *Ropalidia* (Jeanna 1975). the Tibbetts (2004) proposed that a second factor, nest-founding behavior, may be linked to signaling in *Polistes*. She describes three nest-founding strategies: single foundress species and obligate nest-founding species do not display signals. Single foundresses would not need to display signals because she is always the dominant individual on the nest. In obligate nest-founding species, the dominant queen monopolizes the nest and there appears to be little interaction amount the foundresses, so signals may not be useful. Flexible nest-founding species have nests that vary from single to multiple foundresses. These species display more complex social behaviors such as partitioning egg laying and food among the ranks (Tibbetts & Reeve 2000). Signals are present in many of these species. Signaling may be used to manage conflicts between queens by displaying quality signals, or in the case of *P. fuscatus*, remembering the encounters all

together. Interestingly, *M. mexicanus* also shows flexible nesting strategies with multiple foundresses, but lacks signals (Litte 1976). We propose a third factor, body size, and the constraints it poses on display area, also affect the evolution of visual communication in social wasps. This hypothesis may explain why *M. mexicanus,* a small wasp which has flexible nesting strategies and open nests, does not use visual signals. Our model can be expanded to other species of flexible nest-founding species.

Research often looks at effects of environment or body size on the production of acoustic signals. These two factors are often constraints of acoustic signaling ability in taxa such as insects and birds (Ryan 1985, Bennet-Clark 1998, Ballentine 2006). However, there is very little research looking at limitations of signal production in other sensory systems. We have found evidence that body size could limit visual signaling potential in social wasps. In visual communication, body size should play an important role in species with signal patches like *Polistes*. Future studies should examine the effects of body size on visual signaling in a wider variety of genera that share similar patterns of signaling and range of body sizes that we see in social wasps. Body size could also be a factor of signaling potential in species which use other communication systems such as chemicals and possibly electrocommunication.

In this study, we found that signaling most likely evolved against the background of an already-acute visual system in Vespids. Furthermore, we have shown that body size has a great influence on signaling potential. This may have affected the evolution of visual communication in social wasps. There is currently little research relating size of signaling area to signaling potential. Reanalysis of signaling potential and sensory systems in other insects or other taxa could aid our understanding of the distribution of signals across taxa and modalities. Larger emphasis should be placed on exploring communication evolution by looking at how sensory systems and their sensory systems evolve in response to signals. Exploring both of these areas in greater detail may give way to a better understanding of communication evolution.

REFERENCES

Andersson, M. (1982). Female choice selects for extreme tail length in a widowbird. *Nature* 299: 818-820.

Arevalo, E., Zhu, Y., Carpenter, J.M., & Strassmann, J. E. (2003). *BMC Evolutionary Biology* 4(8): 1-16.

Ballentine, B. (2006). Morphological adaptation influences the evolution of a mating signal. *Evolution* 60(9): 1936-1944.

Barlow, H.B. (1952). The size of ommatidia in apposition eyes. *Journal of Experimental Biology* 667-674.

Basolo, A.L. (1990). Female preference for male sword tail length in the green swordtail, *Xiphophorus helleri* (Pisces: Poecillidae). *Animal Behaviour* 40(2): 332-338.

Bennet-Clark, H.C. (1998). Size and scale effects as constraints in insect sound communication. *Philosophical Transactions the Royal Society* 353(1367): 407-419.

Bradbury, J.W. & Vehrencamp, S.L. (1999). Economic models of animal communication. *Animal Behaviour* 59: 259-268.

Brooke, M. de L., Hanley, S. & Laughlin, S.B. (1999). The scaling of eye size with body mass in birds. *Proceedings of the Royal Society B* 266(1417): 405-412.

Christy, J.H., Baum, J.K. & Backwell, P.R.Y (2002). Attractiveness of sand hoods built by male fiddler crabs, *Uca musica*: test of a sensory trap hypothesis. *Animal Behaviour* 66(1): 89-94.

Cocroft, R.B & Rodriguez, R.L. (2005). The behavioral ecology of insect vibrational communication. *BioScience* 55(4): 323-334.

Dani, F.R., Fratini, S., & Turillazzi, S. (1996). Behavioural evidence for the involvement of Dufour's gland secretion in nestmate recognition in the social wasp Polistes dominulus (Hymenoptera: Vespidae). *Behavioral Ecology and Sociobiology* 38: 311-319.

Dapparto, L., Sledge, F. M, &Turillazzi, S. (2005). Dynamics of cuticular chemical profiles of *Polistes dominulus* workers in orphaned nests (Hymenoptera, Vespidae). *Journal of Insect Phsiology* 51: 969-973.

Desutter-Grandcolas, L. (2002). Phylogeny and the evolution of acoustic communication in extant Ensifera (Insecta, Orthoptera). *Zoological Scripta* 32(6): 525-561.

Endler, J.A. (1993). Some general comments on the evolution and design of animal communicative systems. *Philosophical Transactions: Biological Sciences* 340(1292): 212-225.

Endler, J.A. & Basolo, A.L. (1998). Sensory ecology, receiver biases and sexual selection. *Tree* 13(10): 415-420.

Fullard, J.H. (1988). The tuning of moth ears. *Experientia*3 44: 423-428.

Gerhardt, H.C. (1994). The evolution of vocalization in frogs and toads. *Annual Review of Ecology and Systematics* 25: 293-324.

Greiner, B. (2006). Visual adaptations in the night-active wasp *Apoica pallens. The Journal of Comparative Neurology* 495: 255 – 262.

Greiner, B., Ribi, W.A, & Warrant, E. J. (2004). Retinal and optical adaptations for nocturnal vision in the halictid bee *Megalopta genalis. Cell and Tissue Research* 316: 377-390.

Guilford, T. & Dawkins, M.S. (1991). Receiver psychology and the evolution of animal signals. *Animal Behaviour* 42: 1-14.

Herzner, G., Schmitt, T., Linsenmair, K.E. & Strohm. E. (2005). Prey recognition by females of the European beewolf and its potential for a sensory trap. *Animal Behaviour* 70: 1411-1418.

Hines, H.M, Hunt, J.M., O'Connor, T.K., Gillesple, J.J, & Cameron, S.A. (2006). Multigene phylogeny reveals eusociality evolved twice in Vespid wasps. *PNAS* 104(9): 3295-3299.

Hölldobler, B. & Carlin, N.F. (1987). Anonymity and specificity in the chemical communication signals of social insects. *Journal of Comparative Physiology A* 161: 567-581.

Howland, H.C., Merola, S. & Basarab, J.R. (2004). The allometry and scaling of the size of vertebrate eyes. *Vision Research* 44(17): 2043-2065.

Ishay, J. (1975). Hornet nest architecture. *Nature* 253: 41-42.

Jackson, B.D & Morgan, E.D. (1993). Insect chemical communication: pheromones and exocrine glands of ants. *Chemoecology* 4: 125-144.

Jander, U. & Jander, R. (2001). Allometry and resolution of bee eyes (Apoidea). *Arthropod Structure & Development* 30(3): 179-193.

Jang, Y. & Greenfield, M.D. (1995) Ultrasonic communication and sexual selection in wax moths: female choice based on energy and asynchrony of male signals. *Animal Behaviour* 51: 1095-1106.

Jeanna, R.L. (1975). The adaptiveness of social wasp nest architecture. *The Quarterly Review of Biology* 50(3): 267-287.

Kelber, A., Jonsson, F., Wallen, R., *et al.* (2011). Hornets can fly at night without obvious adaptations of eyes and ocelli. *PLOSone* 6(7): 1-9.

Kelber, A., Warrant, E.J., Pfaff, M., Wallen, R., *et al.* (2005). Light intensity limits foraging activity in nocturnal and crepuscular bees. *Behavioral Ecology* 17(1): 63-72.

Land, M.F. (1993). The design of compound eyes. In C. Blakemore, K. Adler & M. Pointon, *Vision: Coding and Efficiency* 55-65. Cambridge: Cambridge University Press.

Land, M.F. (1997). Visual acuity in insects. *Annual Review of Entomology* 42: 147-177.

Land, M.F. & Eckert, H. (1985). Maps of the acute zones of fly eyes. *Journal of Comparative Physiology* 156: 525-538.

Land, M.F. & Nilsson D.E (2002) *Animal Eyes.* Oxford University Press. Oxford, U.K.

Leal, M. & Fleishman, L.J. (2004). Differences in the visual signal design of detectability between allopatric populations of *Anolis* lizards. *The American Naturalist* 163(1): 26-39.

Litte, M. (1977). Behavioral ecology of the social wasp, *Mischocyttarus mexicanus. Behavioral Ecology and Sociobiology* 2: 229-246.

Lyall, A.H. (1957). The growth of trout retina. *Quarterly Journal of Microscopical Science* 98(1): 101-110.

Matthews, R.W. & Matthews, J.R. (2010). *Insect Behavior.* Springer Science+Business Media B.V.

Merry, J.W., Morehouse, N.I., Yturralde, K. & Rutowski, R.L. (2005). The eyes of a patrolling butterfly: Visual field and eye structure in the orange sulphur, *Colias eurytheme* (Lepidoptera, Pieridae). *Journal of Insect Physiology* 52: 240-248.

Mollon, J.D. (1989). "Tho' she kneel'd in the place where they grew…" The uses and origins of primate colour vision. *Journal of Experimental Biology* 146: 21-38.

Niven, J.E. & Laughlin, S.B. (2008). Energy limitation as a selective pressure on the evolution of sensory systems. *The Journal of Experimental Biology* 211: 1792-1804.

Osorio, D. & Vorobyev, M. (1996). Colour vision as an adaptation to frugivory in Primates. *Proceedings of the Royal Society* 263: 593-599.

Pickett, K. M. & Carpenter, J.M. (2010). Simultaneous analysis and the origin of eusociality in the Vespidae (Insecta: Hymenoptera). *Arthropod Systematics & Phylogeny* 68(1): 3-33.

Pickett, K.M., Carpenter, J.M. & Wheeler, W.C. (2006). Systematics of *Polistes* (Hymenoptera: Vespidae), with a phylogenetic consideration of Hamilton's haplodiploidy hypothesis. *Annales Zoologici Fennici* 43: 390-406.

Rossel, S. (1979). Regional differences in photoreceptor performance in the eye of praying mantis. *Journal of Comparative Physiology* 131: 95-112.

Rutowski, R.L., Gislen, L. & Warrant, E.J. (2008). Visual acuity and sensitivity increase allometrically with body size in butterflies. *Arthropod Structure & Development* 38: 91-100.

Rutowski, R.L. & Warrant, E.J. (2002). Visual field structure in the Empress Leilia, *Asterocampa leilia* (Lepodoptera, Nymphalidae): dimensions and regional variation in acuity. *Journal of Comparative Physiology A* 188: 1-12.

Ryan, M.J. & Brenowitz, E.A. (1985). The role of body size, phylogeny, and ambient noise in the evolution of bird song. *The American Naturalist* 126(1): 87-100.

Seyfarth, R.M. & Cheney, D.L. (2003). Signalers and receivers in animal communication. *Annual Review of Psychology* 54: 145-173.

Sheehan, M.J. & Tibbetts, E.A. (2008). Robust long-term memory in a paper wasp. *Current Biology* 18(18): R851-R852.

Sheehan, M.J. & Tibbetts, E.A. (2010). Selection for individual recognition and the evolution of polymorphic identity signals in *Polistes* paper wasps. *Journal of Evolutionary Biology* 23(3): 570-577.

Snyder, A.W., Stavenga, D.G. & Laughlin, S.B. (1977). Spatial information capacity of compound eyes. *Journal of Comparative Physiology* (116): 183-207.

Tibbetts, E.A. (2002). Visual signals of individual identity in the wasp *Polistes fuscatus. Proceedings of the Royal Society B* 269(1499): 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 B* 271: 1955-1960.

Tibbetts, E.A. & Dale, J. (2004). A social enforced signal of quality in a paper wasp. *Nature* 432: 218-222.

Tibbetts, E.A. & Lindsay, R. (2008). Visual signals of status and rival assessment in *Polistes dominulus* paper wasps. *Biology Letters* 4: 237-239.

Tibbetts, E.A. & Reeve, H.K. (2000). Aggression and resource sharing among foundresses in social wasp *Polistes dominulus*: testing transactional theories of conflict. *Behavioral Ecology and Sociobiology* 48(5): 344-352.

Tibbetts, E.A. & Sheehan, M.J. (2011). Facial patterns are a conventional signal of agnostic ability in *Polistes exclamans* paper wasps. *Ethology* 117: 1138-1146.

Virant-Doberlet, M. & Cokl, A. (2004). Vibrational communication in insects. *Neotropical Entomology* 33(2): 121-134.

Wiley, R.H. (2006). Signal Detection and Animal Communication. *Advances in the Study of Behavior* 36: 217-247.

Wiley, R.H. & Richards, D.G. (1978). Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. *Behavioral Ecology and Sociobiology* 3(1):69-94.

Table 1. Collection locations for each study species. Except for *M. mexicanus* and *P. annularis,* all individuals were taken from different nests. It is unknown if individuals of hornet species, *V. crabro* and *V. vulgaris,* were from different nests.

Species	Individual 1	Individual 2	Individual 3	Individual 4
Mischocyttarus mexicanus	S. Florida (2011)	S. Florida (2011)	S. Florida (2011)	S. Florida (2011)
Polistes annularis	S.E Louisiana (2011)	S.E Louisiana (2011)	S.E Louisiana (2011)	S.E Louisiana (2011)
Polistes apachus	S. Texas (2011)	S. Texas (2011)	C. Texas (2011)	S. Texas (2011)
Polistes bahamensis	S. Florida (2011)	S. Florida (2011)	S. Florida (2011)	S. Florida (2011)
Polistes bellicosus	S. Louisiana (2011)	S. Louisiana (2011)	S. Louisiana (2011)	S. Louisiana (2011)
Polistes dominulus	E. Michigan (2011)	E. Michigan (2011)	E. Michigan (2011)	E. Michigan (2011)
Polistes dorsalis	S.E Louisiana (2011)	S. Florida (2011)	W. Florida (2011)	Florida (2011)
Polistes exclamans	W. Florida (2011)	W. Florida (2011)	W. Florida (2011)	W. Florida (2011)
Polistes fuscatus	E. Michigan (2009)	S.W. Pennsylvania (2008)	Massachusetts (2010)	Central Pennsylvania (2010)
Polistes major	E. Florida (2011)	S. Florida (2011)	W. Florida (2011)	S. Texas (2011)
Polistes metricus	S. Louisiana (2011)	N. Ohio (2011)	N. Ohio (2011)	N. Ohio (2011)
Vespa crabro[1]	S. Sweden (2011)	S. Sweden (2011)	S. Sweden (2011)	S. Sweden (2011)
Vespula vulgaris[1]	S. Sweden (2011)	S. Sweden (2011)	S. Sweden (2011)	S. Sweden (2011)

Data of species not collected during this study were obtained from:
[1] *Kelber, A. (2011)*

Table 2. Eye morphology data for all study species. Values are species averages with standard deviations. Includes head width, eye height, facets per eye, maximum facet diameter, and the interommatidial angle of *P. fuscatus.*

Species	Eye Height (mm)	Facet Number per eye	Maximum Facet Diameter (µm)	Interommatidial Angle(degrees)
Mischocyttarus mexicanus	1.84±0.02	4805±200	25.63±0.49	-
Polistes annularis	3.13±0.06	7991±283	34.03±0.63	-
Polistes apachus	2.69±0.06	7908±243	28.83±0.47	-
Polistes bahamensis	2.53±0.03	6968±365	30.16±1.25	-
Polistes bellicosus	2.67±0.14	7979±163	28.83±0.75	-
Polistes dominulus	2.40±0.09	6381±333	26.36±0.46	-
Polistes dorsalis	2.23±0.04	6381±300	25.90±0.78	-
Polistes exclamans	2.36±0.08	6187±463	28.38±0.43	-
Polistes fuscatus	2.56±0.10	6875±434	29.24±1.34	1.4
Polistes major	2.53±0.11	7564±191	28.65±1.37	-
Polistes metricus	2.63±0.08	7544±796	30.15±1.01	-
Vespa crabro[1]	3.7±0.1	-	35.20±2.4	-
Vespula vulgaris[1]	2.2±0.1	-	27.00±2.9	-

Data of species not collected during this study were obtained from:
[1] *Kelber, A. (2011)*

Table 3. Body morphology data for all study species. Values are species averages with standard deviations. Includes head width, antenna segment length, femur length, clypeus width, and clypeus height.

Species	Head Width (mm)	Antenna (mm)	Femur (mm)	Clypeus Width (mm)	Clypeus Height (mm)
Mischocyttarus mexicanus	2.7±0.25	0.60±0.26	2.36±0.13	1.06±0.04	0.89±0.10
Polistes annularis	5.18±0.12	1.56±0.04	5.38±0.12	2.22±0.05	1.94±0.05
Polistes apachus	4.23±0.10	1.23±0.04	4.42±0.22	1.92±0.09	1.85±0.11
Polistes bahamensis	3.88±0.02	1.21±0.02	3.82±0.03	1.68±0.04	1.55±0.07
Polistes bellicosus	4.01±0.19	1.18±0.05	4.05±0.25	1.83±0.11	1.77±0.09
Polistes dominulus	3.62±0.07	0.92±0.03	3.12±0.05	1.63±0.04	1.43±0.8
Polistes dorsalis	3.36±0.12	0.970.04	3.15±0.14	1.45±0.04	1.34±0.03
Polistes exclamans	3.595±0.11	1.16±0.04	3.12±0.75	1.65±0.24	1.49±0.06
Polistes fuscatus	3.93±0.13	1.13±0.6	3.68±0.17	1.79±0.09	1.73±0.12
Polistes major	4.25±0.14	1.22±0.43	4.13±0.10	2.01±0.12	1.96±0.09
Polistes metricus	4.09±0.10	1.22±0.05	3.87±0.17	1.82±0.10	1.78±0.13
Vespa crabro[1]	5.6	-	-	-	-
Vespula vulgaris[1]	3.2	-	-	-	-

Data of species not collected during this study were obtained from:
[1] Kelber, A. (2011)

Table 4. Multivariate generalized linear model of *Polistes* species comparing signals to PCA factor score for body size.

Multivariate Tests

Effect	Hypothesis df	Error df	F	p-value
Presence of Signals	3	4	0.986	0.484
PCA Factor Score for Body Size	3	4	7.825	0.038
Signals*PCA Factor Score	3	4	3.511	0.128

Tests of Between-subjects Effects

Source	Dependent Variable	df	F	p-value	Adjusted r^2 Value
Corrected Model	Log(Eye Height)	3	13.103	0.005	0.801
	Log(Facet Number)	3	4.516	0.055	0.540
	Log(Max Facet Diameter)	3	9.646	0.010	0.742
Presence of Signals	Log(Eye Height)	1	0.387	0.557	
	Log(Facet Number)	1	0.109	0.753	
	Log(Max Facet Diameter)	1	0.014	0.909	
PCA Factor Score for Body Size	Log(Eye Height)	1	22.68	0.003	
	Log(Facet Number)	1	5.491	0.058	
	Log(Max Facet Diameter)	1	15.137	0.008	
Signals & PCA Factor Score	Log(Eye Height)	1	0.631	0.457	
	Log(Facet Number)	1	0.588	0.472	
	Log(Max Facet Diameter)	1	0.005	0.949	

Table 5. Estimated number of perceivable signals variants by Polistine wasps at a distance of 1 cm, 0.5 cm, and 2 cm. Table is sorted in increasing clypeus width. Estimated signal variants were rounded down to the nearest number.

				Perceivable Signal Variants						
Vespid Species	Estimated Interommatidial Angles (degrees)	Clypeus Height (cm)	Clypeus Width (cm)	0.5 cm (Clypeus Height)	0.5 cm (Clypeus Width)	1 cm (Clypeus Height)	1 cm (Clypeus Width)	2 cm (Clypeus Height)	2 cm (Clypeus Width)
M. mexicanus	1.58 - 1.76	0.09	0.11	5 - 6	6 - 7	2 - 3	3	1	1
P. dorsalis	1.57 - 1.73	0.13	0.14	8-9	9 - 10	4	4 - 5	2	2
P. dominulus	1.54 - 1.69	0.14	0.1	9-10	11 - 12	4 - 5	5 - 6	2	2 - 3
P. exclamans	1.44 - 1.49	0.15	0.16	11	12 - 13	5	6	2	3
P. bahamensis	1.31 - 1.35	0.16	0.17	13 - 14	14	6	7	3	3
P. fuscatus	1.4*	0.17	0.18	14	14	7	7	3	3
P. metricus	1.31 - 1.35	0.18	0.18	15	15	7	7	3	3
P. bellicosus	1.42 - 1.44	0.18	0.18	14	14	7	7	2	2 - 3
P. apachus	1.42 - 1.44	0.18	0.19	14 - 15	15	7	7	3	3
P. major	1.43 - 1.46	0.2	0.20	15	15 - 16	7	7 - 8	3	3 - 4
P. annularis	0.92 - 1.1	0.19	0.22	19 - 24	21 - 27	9 - 12	10 - 13	4 - 6	5 - 6

*measured value

Figure 1. Body and eye morphology measurements used in this study. (a) Shows the cuts made in each acrylic eye replica before flattening. (b) The locations of head and eye measurements. Head width (solid red) was taken at the widest distance on the head. Eye height (solid blue) was from the dorsal to ventral part of the eye. Clypeus width (dotted blue) was measured at the widest portion. Clypeus height (dotted red) was measured along the midline from each point of the top and bottom. (c) First and longest segment of the antenna flagellum was measured for antenna length (purple). (d) The longest distance on the femur was recorded a femur length (pink).
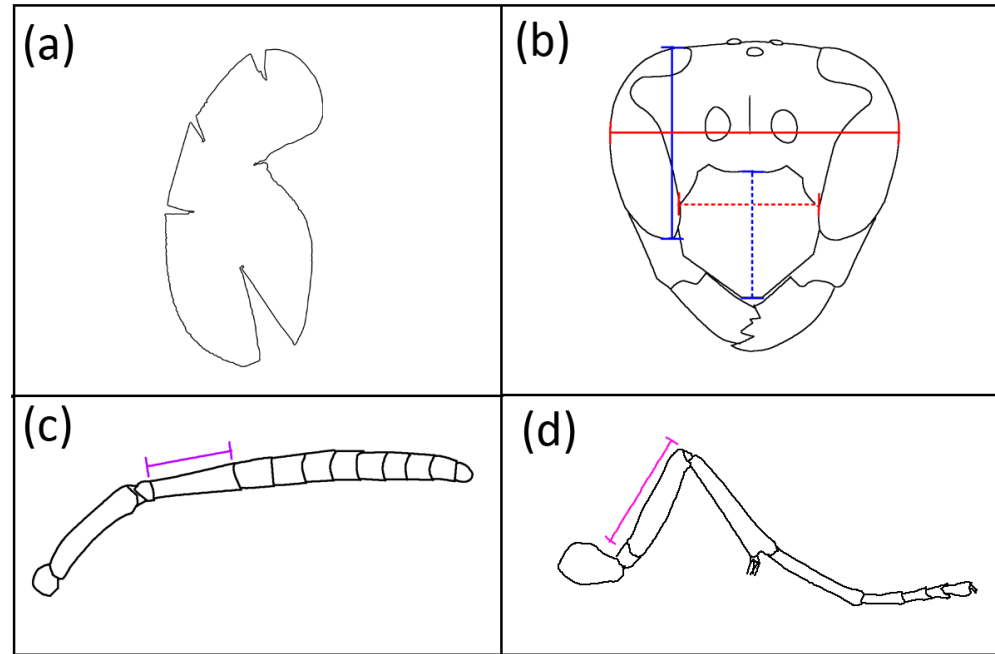
Figure 2. Eye maps of eight *Polistes* and *Mischocyttarus mexicanus*. Circles with the largest possible diameter were fit into each facet to create a color map of facet sizes. Each color represents a different facet size. Vespids all share similar eye morphology, varying only in facet size. The eyes are irregularly shaped, somewhat ovular stretching from the dorsal to ventral regions of the head, with an indent on the frontal-dorsal region. As seen, the smallest facets are clustered at the dorsal region of the eye, near the ocelli. Facets also decreased in size on the borders of the eye. Notably, the areas with the largest facets, the acute zone, are located in the frontal-ventral region. Very large species, such as *P. annularis* and *P. apachus* have two regions with large facets, one located on the front of the eye, and the other on the outer region of the eye which is normally wrapped around the side of the head. The smallest species, *Mischocytarrus* has a comparatively large acute zone.
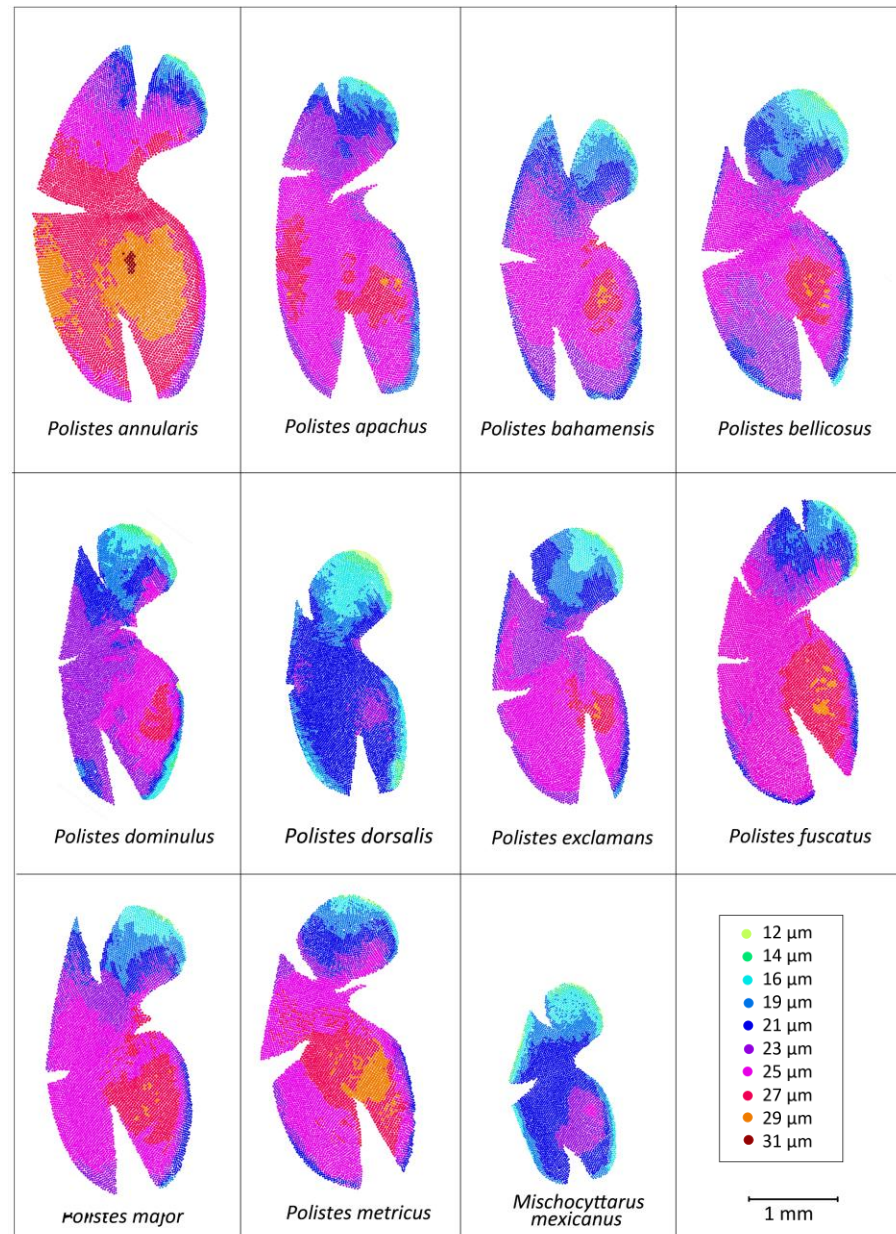

18

Figure 3. Diagram of the relationship between interommatidial angle ($\Delta\phi$), the distance (d) between the sender and the receiver, and the minimum discrepancy (x) that is necessary between for the receiver to perceive two different signals without aliasing.
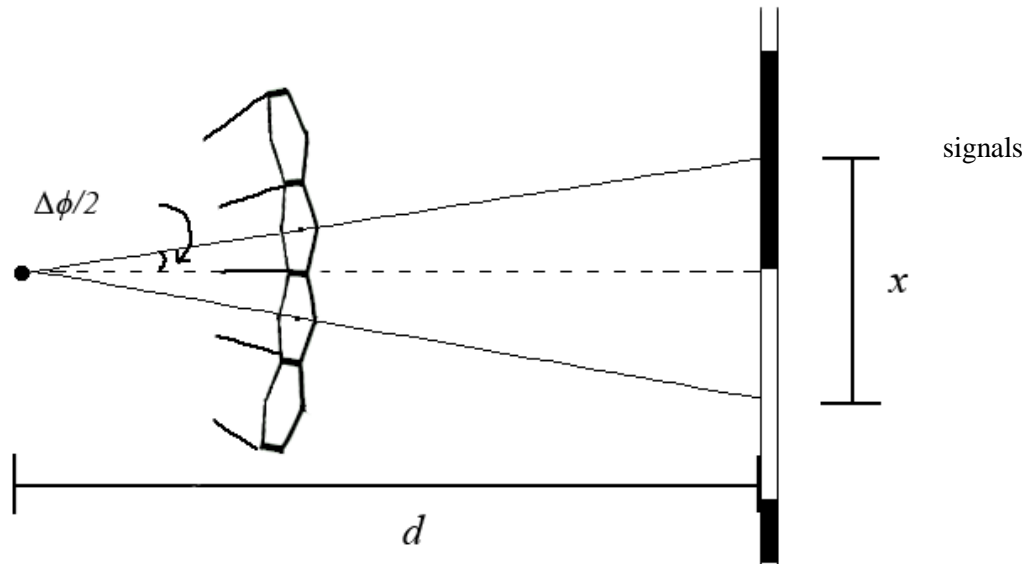
$\Delta\phi/2$

signals

x

d

Figure 4. A comparison of the 11 species collected for the study. Species designated with an asterisk are species which have signals.
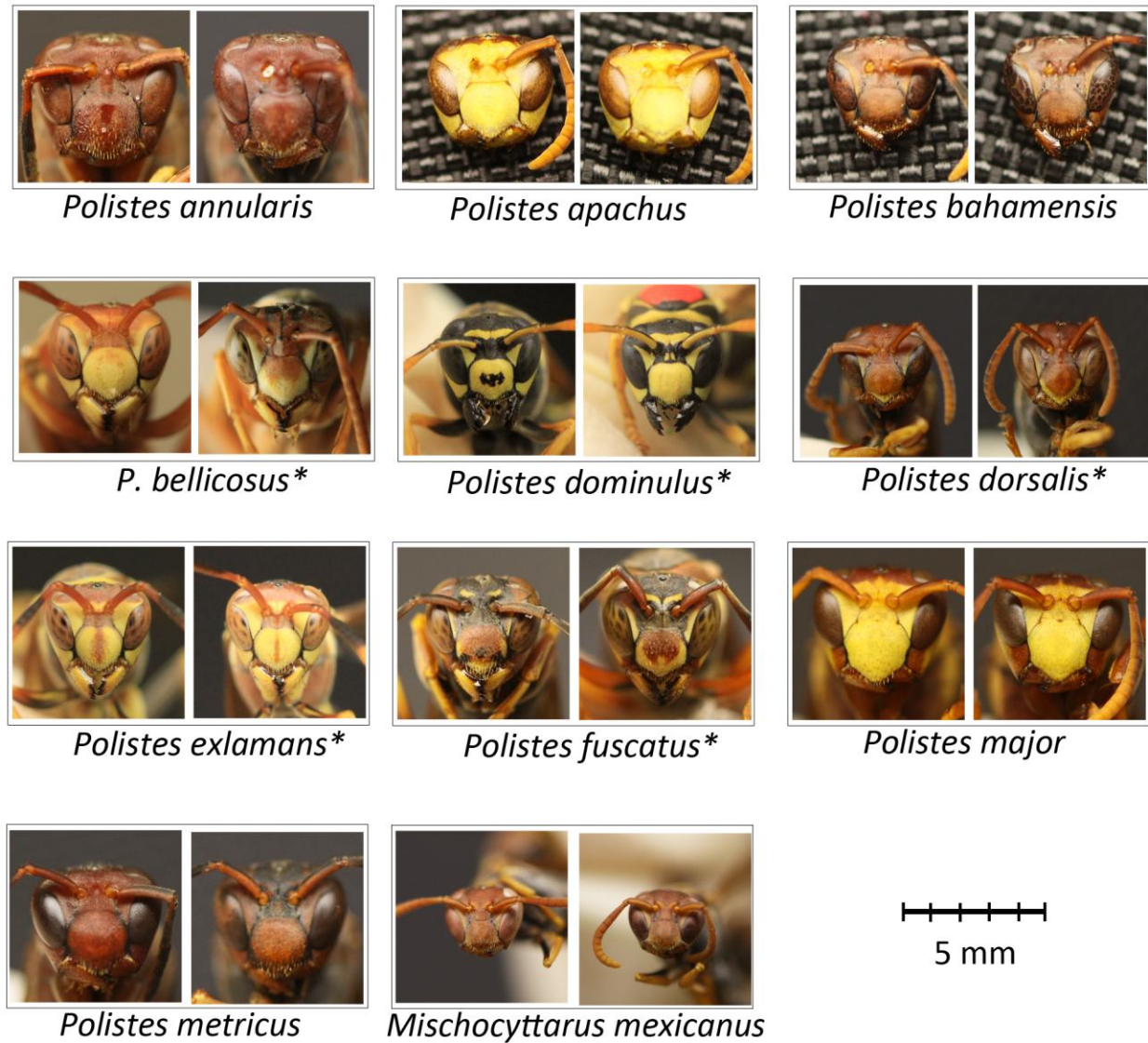

Polistes annularis

Polistes apachus

Polistes bahamensis

P. bellicosus*

Polistes dominulus*

Polistes dorsalis*

Polistes exlamans*

Polistes fuscatus*

Polistes major

Polistes metricus

Mischocyttarus mexicanus

5 mm

Figure 5. Linear regression with individual confidence intervals comparing principal component axis (PCA) factor scores for body size (femur length and antenna segment length) and eye morphology data among species of *Polistes*. Dashed line represents confidence intervals. Signaling and non-signaling species are also represented in the graphs. (a) PCA score vs eye height. (b) PCA score vs facet number. (c) PCA score vs maximum facet diameter.
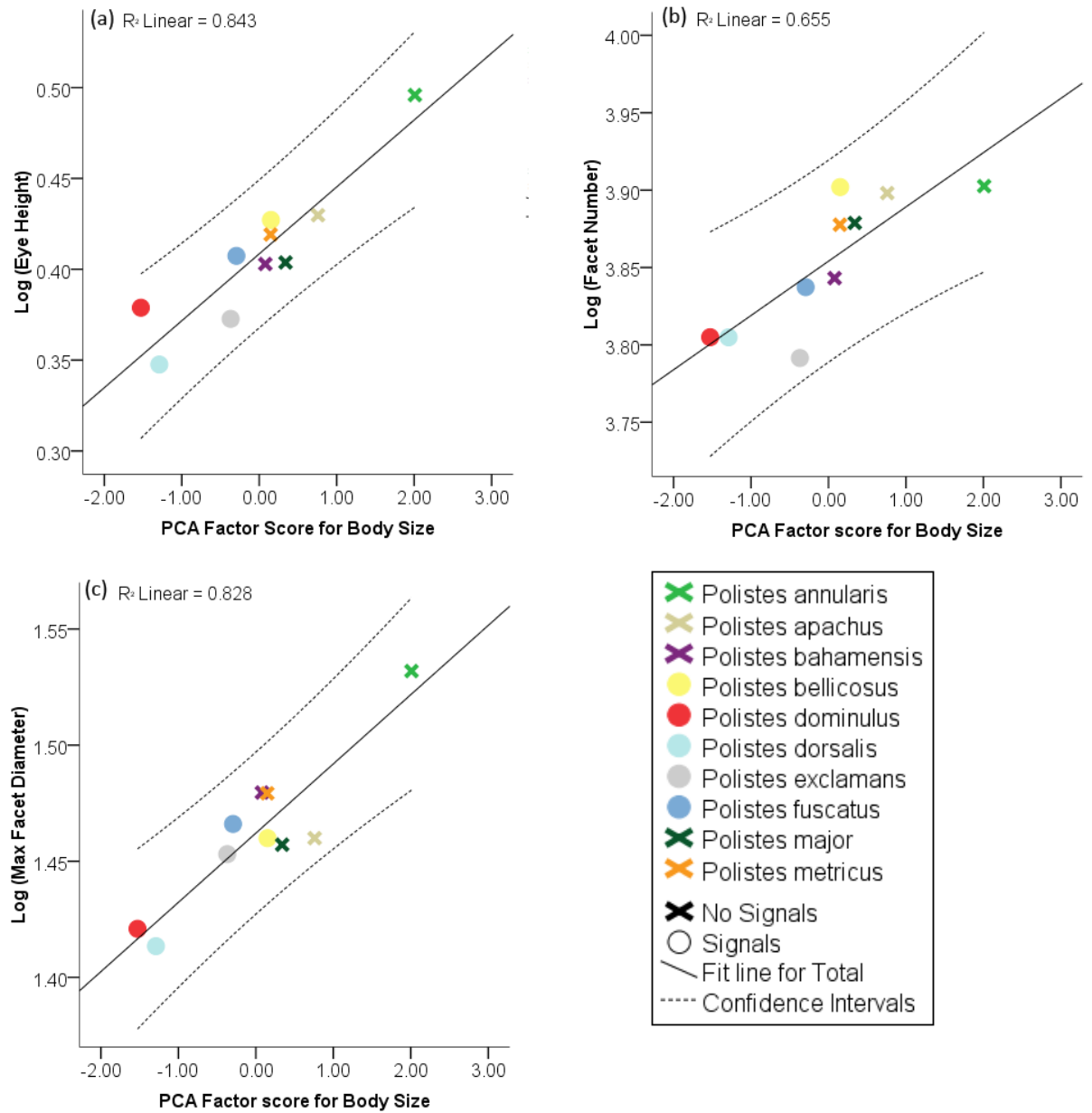
Figure 6. Linear regressions with individual confidence intervals comparing body size (head widths as proxy) and eye morphology data between genera. Dashed line represents confidence intervals. (a) Head width vs eye height. (b) Head width vs maximum facet diameter.
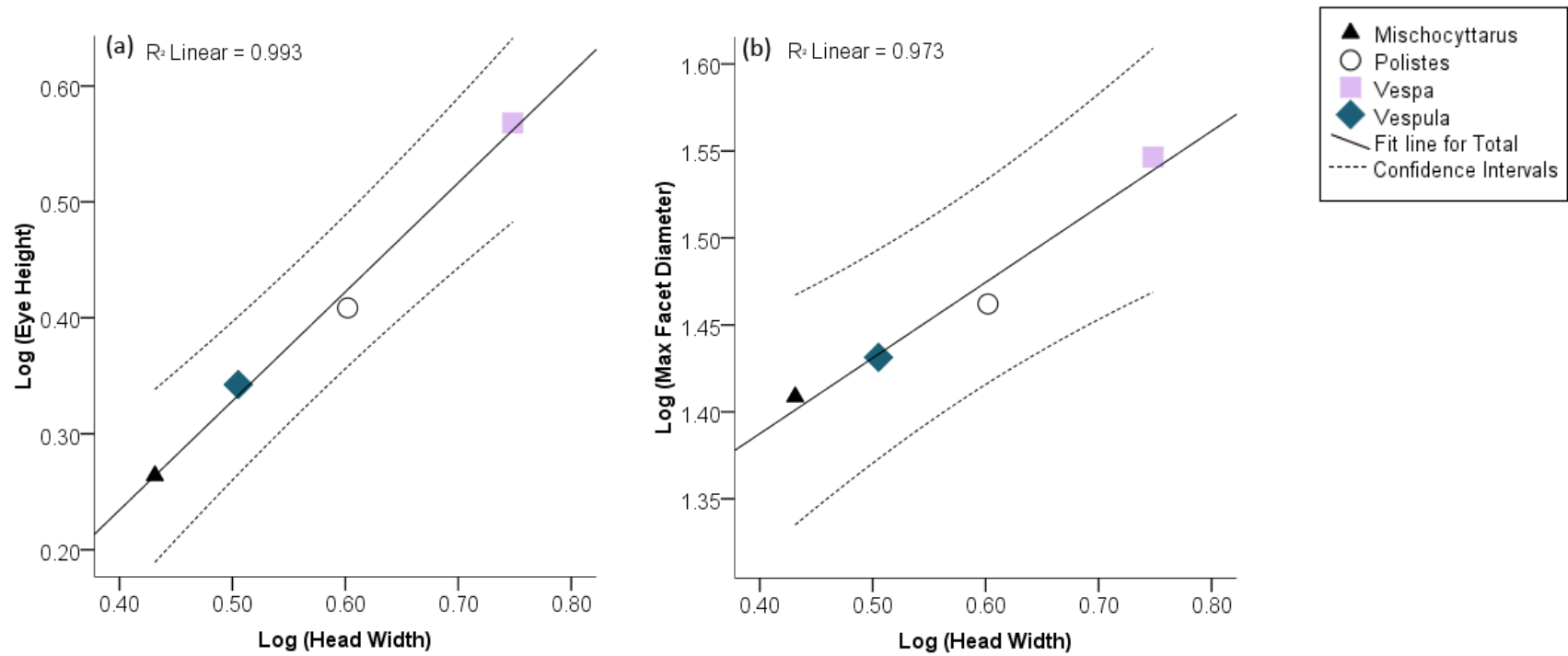
Figure 7. Linear egressions with individual confidence intervals comparing within eye morphology for all species. Dashed line represents confidence intervals. *Mischocytarrus mexicanus, Vespa crabro,* and *Vespula vulgaris* do not have signals. (a) Head width vs facet number. *V. crabro* and *V. vulgaris* were excluded due to lack of data. (b) Eye height vs maximum facet diameter. (c) facet number vs maximum facet diameter.
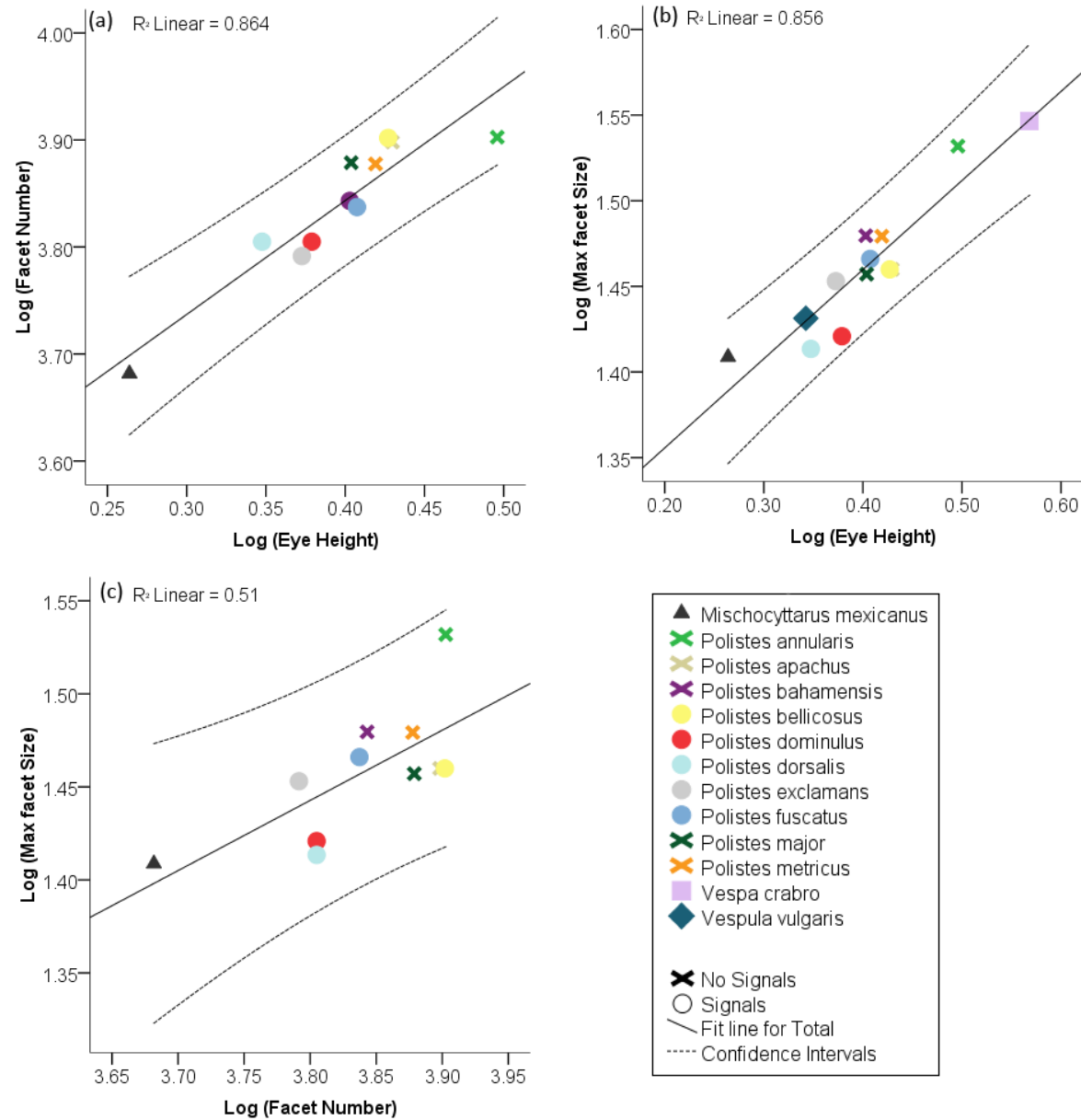
Figure 8. Two angles of a surface model of the relationship between interommatidial angle, clypeus size, and the number of possible distinguishable phenotypes at a distance of 1 cm. X-axis is from 0-3˚. Y-axis is from 0-0.3 cm. Z-axis is from 0-15 differentiable signals. (a) Perceivable signal variants at 1 cm. *Polistes fuscatus* falls into the middle of this model. (b) Figure 6a from different angle to show the graph shape. (c) Perceivable signal variants at 0.5 cm. (d) Perceivable signal variants at 1 cm.

(c)

Clypeus
Size (cm)

Number of Perceivable Signal Variants

Interommatidial Angle (degrees)

(d)

Clypeus
Size (cm)

Number of Perceivable Signal Variants

Interommatidial Angle (degrees)

25