Socially selected ornaments and fitness: Signals of fighting ability in paper wasps are positively associated with survival, reproductive success, and rank

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Abstract

Many animals have ornaments that mediate choice and competition in social and sexual contexts. Individuals with elaborate sexual ornaments typically have higher fitness than those with less elaborate ornaments, but less is known about whether socially selected ornaments are associated with fitness. Here, we test the relationship between fitness and facial patterns that are a socially-selected signal of fighting ability in *Polistes dominula* wasps. We found wasps that signal higher fighting ability have larger nests, are more likely to survive harsh winters, and obtain higher dominance rank than wasps that signal lower fighting ability. In comparison, body weight was not associated with fitness. Larger wasps were dominant over smaller wasps, but showed no difference nest size or survival. Overall, the positive relationship between wasp facial patterns and fitness indicates that receivers can obtain diverse information about a signaler's phenotypic quality by paying attention to socially selected ornaments. Therefore, there are surprisingly strong parallels between the information conveyed by socially and sexually selected signals. Similar fitness relationships in social and sexually selected signals may be one reason it can be difficult to distinguish the role of social versus sexual selection in ornament evolution.

Introduction

Animals use ornaments to make decisions about potential mates and rivals. Sexually selected ornaments are used during competition over resources in a mating context, while non-sexual socially selected ornaments (henceforth socially selected ornaments) are used during competition over non-mating resources (West-Eberhard 1983; Lyon and Montgomerie 2012; Tobias et al. 2012). Sexually selected signals are well-studied and include visual, acoustic, and olfactoral traits across taxa (Andersson 1994; Johnstone 1995). Socially selected signals have received less attention, though numerous examples have been identified, including female ornaments in many taxa (Tobias et al. 2012), black plumage patches in sparrows (Rohwer 1985; Tibbetts and Safran 2009), facial patterns in several species of wasps (Tibbetts 2013), and chameleon color change (Stuart-Fox and Moussalli 2008).

There is some disagreement about whether socially and sexually selected ornaments are shaped by fundamentally similar selective pressures or are distinct (Lyon and Montgomerie 2012; Tobias et al. 2012; West-Eberhard 2014). One way to address this issue is to compare the relationship between ornaments and fitness across signal types. In particular, do individuals with elaborate ornaments have higher fitness than those with less elaborate ornaments? The alternative is that individuals with elaborate ornaments may excel in certain situations (e.g. attain high dominance rank) but perform poorly in other situations (e.g. lower survival) such that fitness is unrelated to ornament elaboration.

Extensive research has shown that individuals with elaborate sexual ornaments have higher fitness and are 'higher quality' in diverse ways than those with less elaborate ornaments (e.g. disease resistance, foraging efficiency, resource defense, heterozygosity, survival, and reproductive success) (Andersson 1994; Moller and Alatalo 1999; Jennions et al. 2001; Maynard Smith and Harper 2003). The specific relationship between sexual ornaments and fitness varies across species and environments (Chaine and Lyon 2008). Nevertheless, there is broadly consistent evidence that individuals with more elaborate sexual ornaments are higher quality and have higher fitness than those with less elaborate sexual ornaments.

Less is known about the relationship between socially selected ornaments and fitness. By definition, socially selected ornaments must be associated with success during aggressive competition, but it is not clear whether these ornaments are linked with overall fitness (Lyon and Montgomerie 2012; Tobias et al. 2012; Tibbetts 2013; Searcy and Nowicki 2005). Individuals with elaborate ornaments may be generally higher quality than those with less elaborate ornaments. Alternatively, there may be tradeoffs; for example, individuals with elaborate socially selected ornaments win fights but have lower survival than those with less elaborate ornaments (Stearns 1989). To our knowledge, there have been no studies testing the relationship between socially selected ornaments and fitness in the wild.

Here, we test the relationship between a socially selected signal and fitness in *Polistes dominula* paper wasps (Fig. 1). *P. dominula* females have variable black facial patterns that are socially selected agonistic signals. Female wasps use facial patterns to minimize the costs of competition with other nest-founding females. Wasps with more broken black facial patterns are more likely to win fights than individuals with less broken facial patterns (Tibbetts and Dale 2004; Tibbetts et al. 2011a) and are avoided by rivals (Tibbetts and Lindsay 2008; Tibbetts et al. 2010). Paper wasp facial patterns evolved via non-sexual social selection (West-Eberhard 1983) to minimize the costs of aggressive competition over resources (Tibbetts 2014). They are not used during mate selection. *Polistes* have mating system where males compete for access to females and females exhibit strong mate choice (Beani 1996). Unlike females, males do not have variable facial patterns. Instead, they have abdominal spots that are a sexually selected signal used during mate choice (Izzo and Tibbetts 2012).

There has been some previous work on the relationship between *P. dominula* facial patterns and fitness-linked traits. Green et al (Green et al. 2013) studied a Spanish population of *P. dominula* and found no relationship between facial patterns and reproductive success, survival and dominance rank. However, there is very low facial pattern variation in Spain and facial patterns may not function as a signal in this population (Green and Field 2011). Thus far, there have been no previous tests of the relationship between fitness and facial patterns in *P. dominula* populations where facial patterns are known to function as agonistic signals. In this study, we tested the link between fitness and facial pattern elaboration in wild populations of *P. dominula* in Michigan, USA, where facial patterns are known to function as agonistic signals (Tibbetts and Lindsay 2008; Tibbetts et al. 2010; Tibbetts et al. 2011a).

Three fitness-linked traits were assessed in this study: the number of cells in the wasp's nest, overwinter survival, and dominance rank. Number of nest cells provides a good proxy for reproductive success in this population, because each nest cell produces one offspring and paper wasps only build one nest during their lifetime (Jandt et al. 2014; personal observation). Overwintering survival is a key aspect of fitness because *P. dominula* gynes are produced at the end of the season, so they must successfully overwinter before they reproduce. Some *P. dominula* found nests alone, but among individuals that cooperate, dominance rank is associated with reproductive success. The dominant foundress in multiple foundress groups has higher fitness than subordinate or solitary foundresses, though subordinates receive some reproduction (Queller et al. 2000; Reeve and Keller 2001). Although nest size, survival, and rank are important aspects of fitness, it is important to note that fitness is multi-faceted, so it is difficult for a single field study to provide complete measures of lifetime fitness (Stearns 1989; Hunt et al. 2004).

In addition to measuring the relationship between agonistic signals and fitness, we also tested whether body weight is associated with fitness. Across a range of species, larger body size is linked with higher fitness, as larger individuals are often preferred as mates, are more successful during competition, and have higher survival and fecundity than smaller individuals (Fairbairn 1997; Nylin and Gotthard 1998). Of course, the large size advantage is not universal (Blanckenhorn 2000). For example, in paper wasps, larger foundresses are often dominant over smaller foundresses (Pardi 1948; Dropkin and Gamboa 1981), but the relationship between dominance rank and body size varies across studies (reviewed in Jandt et al. 2014). Body size is often linked with both fighting ability and fitness, so it provides a useful comparison with agonistic ornamentation: Is body size more or less strongly associated with fitness than socially selected agonistic ornamentation?

Methods

Reproductive Success:

Polistes dominula nest-founding queens were collected from sites around Ann Arbor, Michigan during the pre-worker phase of colony development, from early May to June in 2011 and 2012. All wasp nests in an area were collected, without preference for particular facial patterns. At collection, wasps were weighed on a scale accurate to 0.001g and photographed for facial pattern analysis. 611 nests were analyzed over 2 years (2011-2012).

Reproductive success was assessed as the number of nest cells. In southeastern Michigan, where the nests were collected, nest construction begins synchronously (within one week) in the early spring and each nest cell produces one offspring. As a result, the number of nest cells provides a good proxy for reproductive success when date of collection is accounted for. Larger spring nests produce more workers and therefore more reproductive males and females than smaller spring nests. The disadvantage of measuring nest size in the spring is that a few nests will fail or be usurped before offspring are produced (Nonacs and Reeve 1995). Usurpation or nest failure could obscure fitness relationships, but are unlikely to create new fitness relationships.

Winter survival:

We assessed survival by comparing average characteristics of nest founding queens collected in Ann Arbor, MI across different years. Foundresses have an annual life-cycle, so different years reflect different generations. The life cycle of a nest founding queen involves developing from egg to adult in the summer, overwintering, then founding nests the following spring (Jandt et al. 2014).

The small size and frequent dispersal of paper wasps means that following individual wild wasps over the winter is not possible. However, we can gain insight into survival by comparing characteristics of spring foundress population across years. We measured the face and weight of spring foundresses and compared with 1) temperature during overwintering and 2) temperature during the summer development period. Wasp facial patterns don't change during adulthood. Therefore, if there are fewer wasps with entirely yellow faces after colder winters, it suggests that individuals with entirely yellow faces are less likely to survive colder winters. The alternative is that fewer wasps with entirely yellow faces are produced in the summer before a cold winter. However, that alternative seems unlikely, as future winter weather is not predictable.

Weather data for Ann Arbor, MI were obtained from the Weather Underground data base (http://www.wunderground.com/). We collated temperatures during foundress larval development and overwintering. The average temperature during foundress larval development was quantified as the average temperature from July 1 to September 1 of the year prior to nest foundation. The average low temperature during the three coldest winter months, December 1 to March 1, was used as the average overwintering low temperature.

The survival analysis includes 4028 individuals measured across 8 years (2006, 2008-2014). Pictures of each foundress are not available, so facial pattern was measured as the proportion of wasps with entirely yellow clypeus. Entirely yellow facial patterns signal the lowest fighting ability and are scored as 0 facial pattern brokenness (Tibbetts 2013). The proportion of foundresses with entirely yellow faces is quite variable across years, from 2% to 18 %. Average weight of foundresses each year was also analyzed.

Dominance rank:

In 2010, the dominance ranks of foundresses on nests that contained multiple foundresses were measured by observing aggressive interactions among individually marked cofoundresses for at least 2 hours, longer if ranks were not immediately apparent. Dominance ranks were determined by mounting behavior. During a mount, the dominant positions itself above the subordinate and drums antennae on the subordinate. The subordinate lowers her antennae when receiving a mount. Wasps only mount individuals that are subordinate to them in the dominance hierarchy (West-Eberhard 1969). In a few cases, it was difficult to distinguish between the rank of two lower ranked foundresses; these wasps were scored as tied. 43 nests from 2010 were included in the dominance analysis. Facial pattern brokenness and weight were measured for each foundress.

Facial pattern brokenness analysis

We assessed the facial pattern of wasps by analyzing a digital picture of the wasp's face with *Adobe Photoshop*. Facial patterns do not change during a wasp's lifetime. A wasp's facial pattern “brokenness” is the best predictor of dominance and takes into account the number, size, and shape of black spots on the wasp’s clypeus (Fig. 1) (Tibbetts 2010; Tibbetts et al. 2010; Tibbetts et al. 2011a). To calculate brokenness, the area of the clypeus containing the population-wide badge variability was converted into a 30×60 pixel bitmap. Then, the number of pixels containing black pigment within each vertical column along the horizontal length of the clypeus was counted. We were interested in the total disruption of the black facial pattern, so we calculated the standard deviation of the black pigment deposition from pixels 5 to 55 along the horizontal gradient of the 60-pixel clypeus. We excluded the first and last 5 pixels from the brokenness analysis because the edges of the clypeus are black. As a result, wasps with black in the first and last five pixels have facial patterns that appear less broken than individuals with black spots that extend to the edge of the clypeus. The standard deviation of the black pigment deposition, or “brokenness” of a wasp’s face measures the amount of disruption in the black coloration and a signal of fighting ability (Tibbetts 2013). Lower values of this index are associated with lower brokenness and lower advertised quality, while higher values are associated with higher brokenness and advertised quality. Facial pattern analysis was performed by a student blind to wasp identity and experimental predictions.

Statistical analyses

All data were analyzed in SPSS v. 21.

Reproductive success: The factors associated with reproductive success were analyzed using a general linear model. The dependent variable was nest size (number of cells). The independent variables were: foundress facial pattern brokenness, foundress weight, date nest size was measured, and whether the nest had a single foundress or multiple foundresses (categorical). Year was included as a categorical random effect in the model to account for any differences in nest size across years. 611 nests were included in the analysis. The data were also analyzed separately within single and multiple foundress nests. Within single foundress nests, an additional analysis was performed without the 3 largest nests. Effect sizes measured as eta squared (η^2) are included. Facial patterns and weight are sometimes weakly correlated (Tibbetts et al. 2011c). Correlation of independent variables can reduce model fit, but the variance inflation factors were less than 1.2 in this data set and 10 is the traditional cut-off. Therefore, model fit is not reduced by collinearity (Zar 2009).

Overwinter survival: Generalized linear models were used to test how foundress characteristics were associated with temperature. Generalized linear models were used because traditional linear models are not appropriate for data like proportions which are unlikely to be normally distributed and are restricted to a small range (0 to 1). In one analysis, the proportion of foundresses with entirely yellow faces in a given year was the dependent variable. Yellow faces signal the lowest fighting ability and have 0 facial pattern brokenness. In the other analysis, the mean weight of foundresses in a given year was the dependent variable. In both analyses, the independent variables were temperature during the summer larval development period and temperature during overwintering. Eight years of data were analyzed, with each year providing one data point.

Dominance rank: The factors associated with dominance rank were analyzed using a generalized linear model. The dependent variable was dominance rank (rank 1, 2, 3, or 4). The independent variables were facial pattern brokenness, weight, and the two way interaction between facial pattern brokenness and weight. Nest was included as a random effect in the model. 112 individuals across 43 nests were included in the analysis.

Results

Within the entire data set, wasps with higher facial pattern brokenness had larger nests than wasps with lower facial pattern brokenness (Table 1, Fig. 2, $F_{1,605}$=13.1, p<0.0001). Although this relationship is highly significant, the effect size is small (η^2=0.021). Nest size was also linked with whether nests had one foundress or multiple foundresses; multiple foundress groups had larger nests than single foundresses ($F_{1,605}$=73.9, p<0.0001, η^2=0.11). Not surprisingly, nests measured later in the season were larger than nests measured earlier in the season ($F_{1,605}$=120.7, p<0.001, η^2=0.17). Year also had an effect on nest size, with nests growing larger in some years than others ($F_{1,605}$=14.2, p<0.0001, η^2=0.023). Finally, body weight was not associated with nest size ($F_{1,605}$=0.41, p =0.52, η^2=0.001).

The results are similar when the data are analyzed separately within nests that contained a single foundress (SF) and nests that contained multiple foundresses (MF). Wasps with higher facial pattern brokenness tended to have larger nests than those with lower facial pattern brokenness (SF, $F_{1,500}$ = 10.6, p = 0.001, η^2=0.021; MF, $F_{1,101}$ = 3.5, p = 0.06, η^2=0.034). Nests sampled later in the season were larger than those sampled earlier (SF $F_{1,500}$=135.9, p=<0.0001, η^2=0.04; MF $F_{1,101}$=8.7, p=0.004, η^2=0.08). Body weight was not associated with nest size (SF $F_{1,500}$ = 1.4, p = 0.23, η^2=0.003; MF, $F_{1,101}$=0.18, p=0.67, η^2=0.002). Nest size varied across years in single but not multiple foundress nests (SF, $F_{1,500}$ = 20.6, p < 0.001, η^2=0.04; MF, $F_{1,101}$=0.11, p=0.73, η^2=0.001). The results are similar if the three largest single foundress nests are excluded from the analysis, indicating that the results are not driven by a few data points (facial pattern $F_{1,497}$ = 7.3, p = 0.007, η^2=0.014; date $F_{1,497}$ = 191, p < 0.001, η^2=0.28; year $F_{1,497}$ = 16.9, p< 0.001, η^2=0.033; weight $F_{1,497}$ = 4.1, p = 0.042, η^2=0.008).

The proportion of foundresses with the entirely yellow facial patterns that signal low fighting ability was positively associated with overwintering temperature (Fig. 3, Wald χ2=3.7 p = 0.05). There were fewer foundresses with entirely yellow faces after colder winters than after warmer winters, suggesting that wasps with entirely yellow faces (signal low agonistic ability) are less likely to survive cold winters than wasps with some black on their faces (signal higher agonistic ability). The average temperature during foundress larval development was not associated with foundress facial patterns (Fig. 3, Wald χ2=0.14, p = 0.90).

Average foundress weight in the spring was not associated with the average minimum temperature during the preceding winter (Fig. 4, Wald χ2=2.7, p = 0.10). Average temperature during larval development was not associated with spring body weight (Wald χ2=0.8, p = 0.37).

Dominance rank was associated with foundress facial patterns (Fig. 5, Wald χ2 = 4.1, p = 0.043), body weight (Wald χ2 = 4.3, p = 0.038), and the interaction between facial patterns and body weight (Wald χ2 = 3.7, p = 0.055). Dominant wasps had more broken facial patterns and larger body weight than subordinate wasps. The interaction occurs because high ranking wasps with low facial pattern brokenness have relatively higher weights.

Discussion

The facial patterns that signal fighting ability in *P. dominula* are linked with three key aspects of fitness: reproductive success, survival, and dominance rank. Wasps with facial patterns advertising higher fighting ability have larger nests than wasps with facial patterns advertising lower fighting ability (Fig. 2). Facial patterns are also associated with surviving harsh conditions; wasps with facial patterns that signal low fighting ability are more likely to die in cold winters than warm winters (Fig. 3). Finally, within wild cofoundress associations, wasps with facial patterns advertising higher fighting ability are dominant over individuals with facial patterns advertising lower fighting ability (Fig. 5), confirming previous studies on the relationship between facial patterns and fighting ability in other experimental contexts (Tibbetts and Dale 2004; Tibbetts and Lindsay 2008; Tibbetts et al. 2010; Tibbetts 2013).

Although facial patterns were consistently associated with fitness, the relationship between body weight and fitness was more complex. High body weight was positively associated with dominance rank, but not nest size or survival. A potential critique of studies with large sample sizes is that they may allow identification of significant relationships with small effect sizes. For example, the relationship between facial pattern and nest size is significant, but weak. Here, the same large sample of wasps was used to test how facial patterns and body weight are linked with fitness, but the analyses yielded very different results. Therefore, the consistent, positive relationship between facial patterns and aspects of fitness is notable.

The results of this study hint at surprising overlap between socially and sexually selected signals. Both are positively associated with fitness and their bearer's overall phenotypic and genetic constitution such that individuals with elaborate ornaments are 'better' than those with less elaborate ornaments (Andersson 1994; Moller and Alatalo 1999; Jennions et al. 2001). Therefore, receivers gain diverse information about the overall quality of senders by paying attention to signals evolved in the context of aggressive competition over non-mating resources. Although our data indicate that receivers could obtain diverse information about overall quality by assessing socially selected signals, little empirical work has tested whether receivers pay attention to socially selected signals in non-competitive contexts. For example, wasps could assess the overall quality of potential cooperative partners via facial patterns and preferentially cooperate with higher quality social partners.

The similar fitness relationships in social and sexually selected signals may be one reason it is often difficult to categorize as ornaments as being socially versus sexually selected. If signals that evolve in the context of aggressive social competition convey information about overall quality, potential mates could use these traits to make decisions about mating partners. As a result, socially selected signals may often be coopted for mate choice such that 'purely' socially selected signals are rare (Berglund et al. 1996).

Previous work in *P. dominula* provides additional evidence that facial patterns are associated with diverse aspects of quality. Wasps with more broken facial patterns are in better physical condition (Tibbetts and Curtis 2007; Tibbetts 2010), emerge from diapause earlier (Tibbetts et al. 2011b), and have higher survival under artificially increased juvenile hormone titers (a hormone that mediates aggressive competition in wasps; Tibbetts and Izzo 2009) than wasps with less broken facial patterns (Tibbetts and Banan 2010). Of course, fitness is multi-faceted and there are often tradeoffs between components of quality (Stearns 1989; Hunt et al. 2004), so there may be fitness trade-offs associated with signaling high fighting ability that have not been identified.

Facial pattern brokenness is positively linked with fitness, so what factors keep the signaling system honest? This study indicates that the signaling system is not an evolutionarily stable strategy (ESS), where individuals that signal high and low fighting ability are pursuing different, but equally fit strategies (Maynard Smith and Harper 1988). Instead, only the 'best' individuals can afford to signal high fighting ability, perhaps because individuals with inaccurate signals suffer social costs that disfavor signal inaccuracy (Tibbetts and Dale 2004; Tibbetts and Izzo 2010).

Multiple factors may contribute to the relationship between nest size and facial pattern elaboration. First, wasps with more broken facial patterns emerge from diapause at cooler temperatures than wasps with less broken facial patterns (Tibbetts et al. 2011b), so they may found nests earlier in the season. Persistent differences in nest size may be due to facial pattern-linked differences in fecundity, parental care, or quality of the nesting location. All these factors have been shown to covary with sexual signal elaboration in other taxa (review in Moller and Jennions 2001), but have not been explicitly tested in socially selected signals.

Facial patterns are also associated with overwinter survival. More foundresses have facial patterns signaling low agonistic ability after warmer winters than after colder winters (Fig. 3). Wasp facial patterns do not change during adulthood. As a result, this relationship suggests that wasps with black spots that signal high agonistic ability are better able to withstand harsh winters than wasps with yellow faces that signal low agonistic ability. Increased survival may occur because wasps use nutritional stores to maintain slightly elevated temperatures during the winter (Weiner et al. 2011) and wasps with black spots are in better nutritional condition than individuals with yellow faces (Tibbetts and Curtis 2007; Tibbetts 2010). Ability to survive the winter is a key aspect of fitness; gynes must overwinter before reproducing. Therefore, wasps with higher facial patterns brokenness experience survival-linked fitness benefits.

The relationship between overwinter temperatures and foundress facial patterns matches previous work on geographic variation in *P. dominula* facial patterns. Wasps from warmer climates have lower facial pattern brokenness than wasps from cooler climates (Tibbetts et al. 2011c), as would be expected if facial pattern brokenness is linked with the ability to withstand cool temperatures. At least some of the geographic difference in facial patterns is due to developmental plasticity, wherein workers and gynes develop faces with higher brokenness in cooler locations (Green et al. 2012). Differential survival of individuals that signal high vs. low agonistic ability also is likely to contribute to the relationship between facial patterns and climate. Insects in cooler locations often experience thermoregulatory benefits of dark coloration (Kingsolver and Huey 1998). However, thermoregulation is unlikely to play an important role in *P. dominula* facial patterns, as a very small amount of black pigment is involved in creating broken facial patterns. Therefore, facial patterns are unlikely to be directly responsible for the increase in winter survival. Instead, facial patterns are associated with overall quality and higher quality wasps deal with cold temperatures better than lower quality wasps.

The results of this study illustrate that facial pattern brokenness is linked with dominance (Fig. 5), matching previous evidence that facial patterns are signals of fighting ability in the United States. The relationship between facial pattern and dominance is weak, but consistent across experiments. In staged contests, wasps with more broken facial patterns are more likely to win fights than those with less broken facial patterns (Tibbetts and Dale 2004; Tibbetts et al. 2011a). Wasps with broken facial patterns are also avoided by rivals (Tibbetts and Lindsay 2008; Tibbetts et al. 2010). In addition, facial pattern brokenness is correlated with juvenile hormone titer, a key hormone mediating aggressive competition (Tibbetts et al. 2011a).

Geographic variation in P. dominula

A previous study of *P. dominula* in Spain, found that neither body size nor facial patterns are linked with survival, reproductive success, or dominance rank. Relationships between dominance rank and facial patterns and/or body size are common in *Polistes* (Pardi 1948; Turillazzi and Pardi 1977; reviewed in Jandt et al. 2014), but Green (Green et al. 2013) found that neither factor was associated with rank. This may be due, in part, to the unusual, highly cooperative behavior in Spain. In a recent survey of 13 *P. dominula* populations, Spain had the highest rate of cooperation (5.2 foundresses per nest), while the other 12 populations averaged 1.4 foundresses per nest. Michigan is slightly lower than average, at 1.2 foundresses per nest. (Sheehan et al. in press). In addition, single foundress colonies in Spain typically fail (Green et al. 2013), while solitary nesting is a common, successful strategy in other US and European *P. dominula* populations (e.g. Nonacs and Reeve 1995; Tibbetts and Reeve 2003). Such differences in cooperation may dramatically influence the dynamics of group formation, including the factors that influence rank.

The differences between Green (Green et al. 2013) and this study may also be due to geographic variation in facial patterns. In Spain, there is relatively little facial pattern variation; approximately 80% of foundresses have the entirely yellow facial patterns that signal low agonistic ability, likely due to the relatively warm climate in southern Spain (Tibbetts et al. 2011c; Green et al. 2013). Outside of Spain, *P. dominula* have higher levels of facial pattern variation, with Michigan wasps having similar facial pattern variation as Ukrainian and Hungarian wasps (Tibbetts et al. 2011c). Low levels of variation reduces statistical power so it is more difficult to detect whether facial patterns are associated with variation in fitness in Spain than other populations. Alternatively, there may be real differences in the role of facial patterns across populations. The low variation means that facial patterns are less likely to provide useful information to receivers, so receivers may not pay attention to variation in facial patterns (Green and Field 2011). Over time, lack of receiver response is predicted to disrupt the reliability of the signaling system. In the future, analysis across multiple populations will be important, as well as common garden experiments to establish the extent of population divergence across *P. dominula* populations.

Overall, the socially selected signal of fighting ability in *P. dominula* is positively linked with fitness; wasps that signal higher fighting ability have higher reproductive success, rank, and survival than those that signal lower fighting ability. In contrast, body weight is not consistently associated with fitness. Although larger wasps are dominant over smaller wasps, large wasps do not have larger nests or higher survival than smaller wasps. The relationship between paper wasp facial patterns and fitness indicates that receivers can obtain information about signaler’s phenotypic quality by paying attention to signals that evolved via social selection to mediate intrasexual aggressive competition. Therefore, there are surprisingly strong parallels between ornaments that mediate competition and choice in mating and non-mating contexts

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Figures:

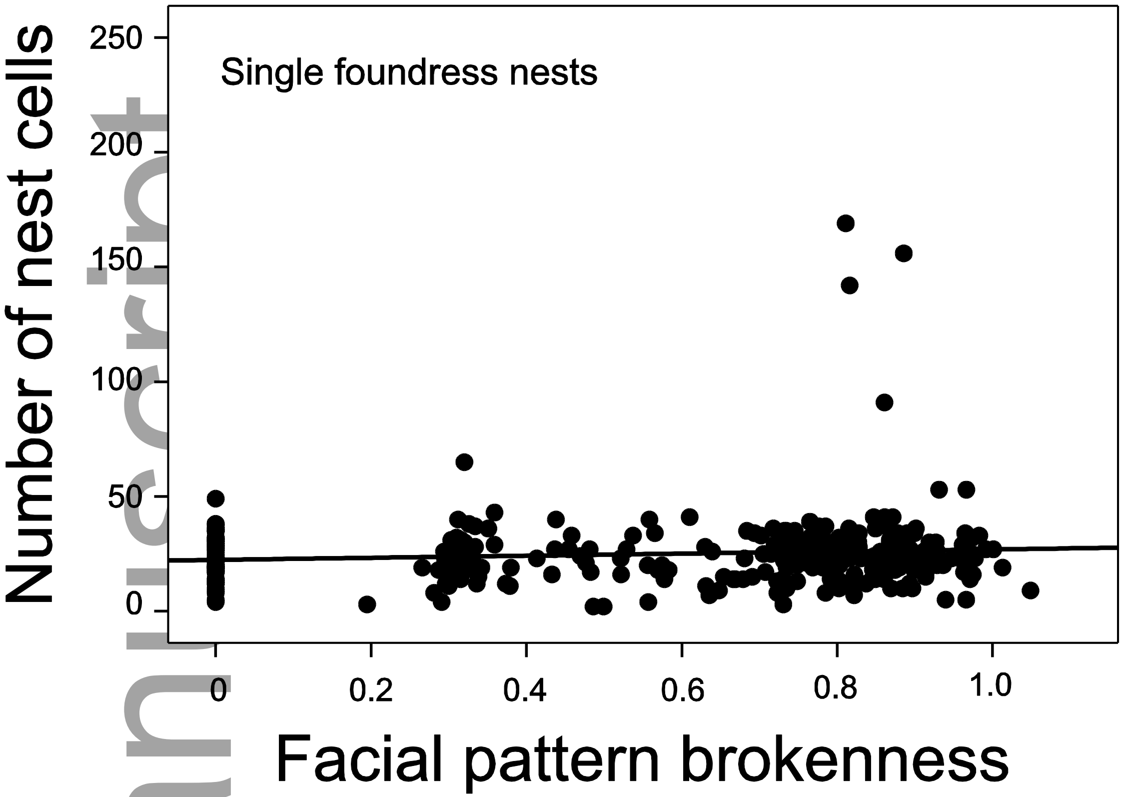
Figure 1, Portraits of *P. dominula*, illustrating variation in the facial patterns that signal agonistic ability.

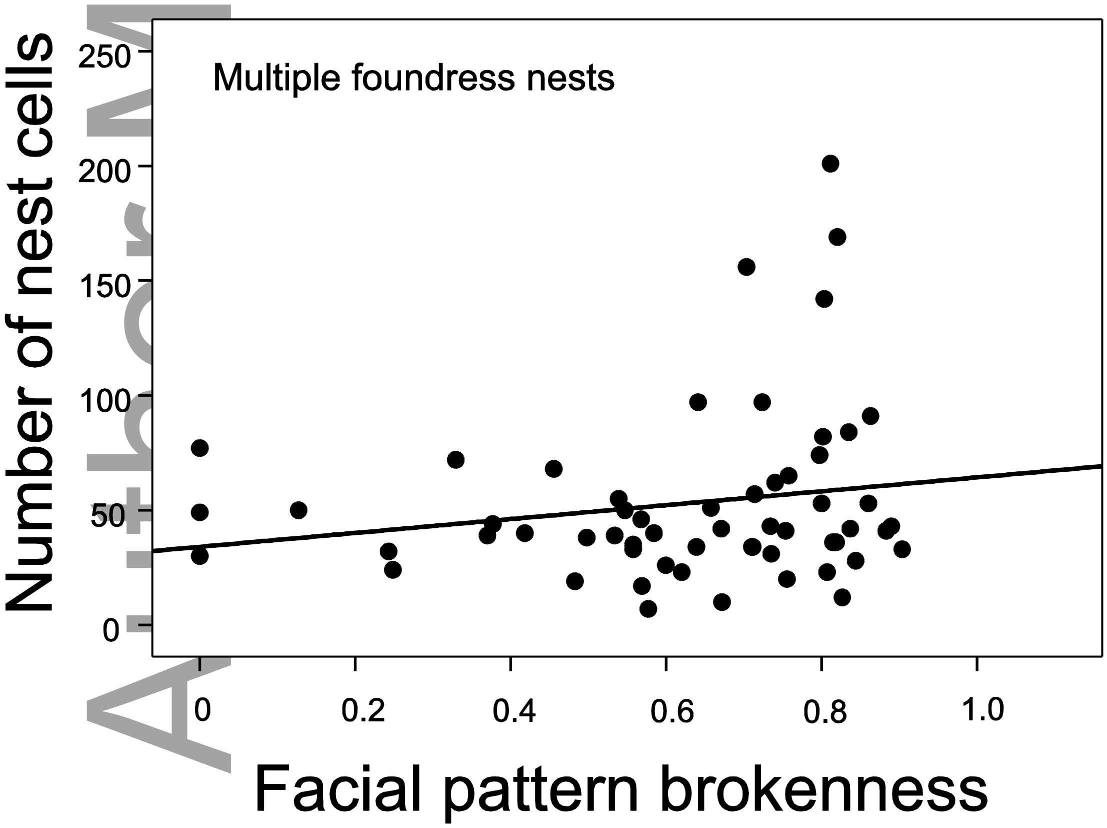
Figure 2, Relationship between facial pattern brokenness (log transformed) and number of nest cells in a) single foundress and b) multiple foundress nests. Foundresses with more broken black facial patterns had larger nests than those with less broken facial patterns. Statistical significance is unaffected when the three largest single foundress nests are excluded from the analysis. Figure shows nests measured between May 24 and June 24.

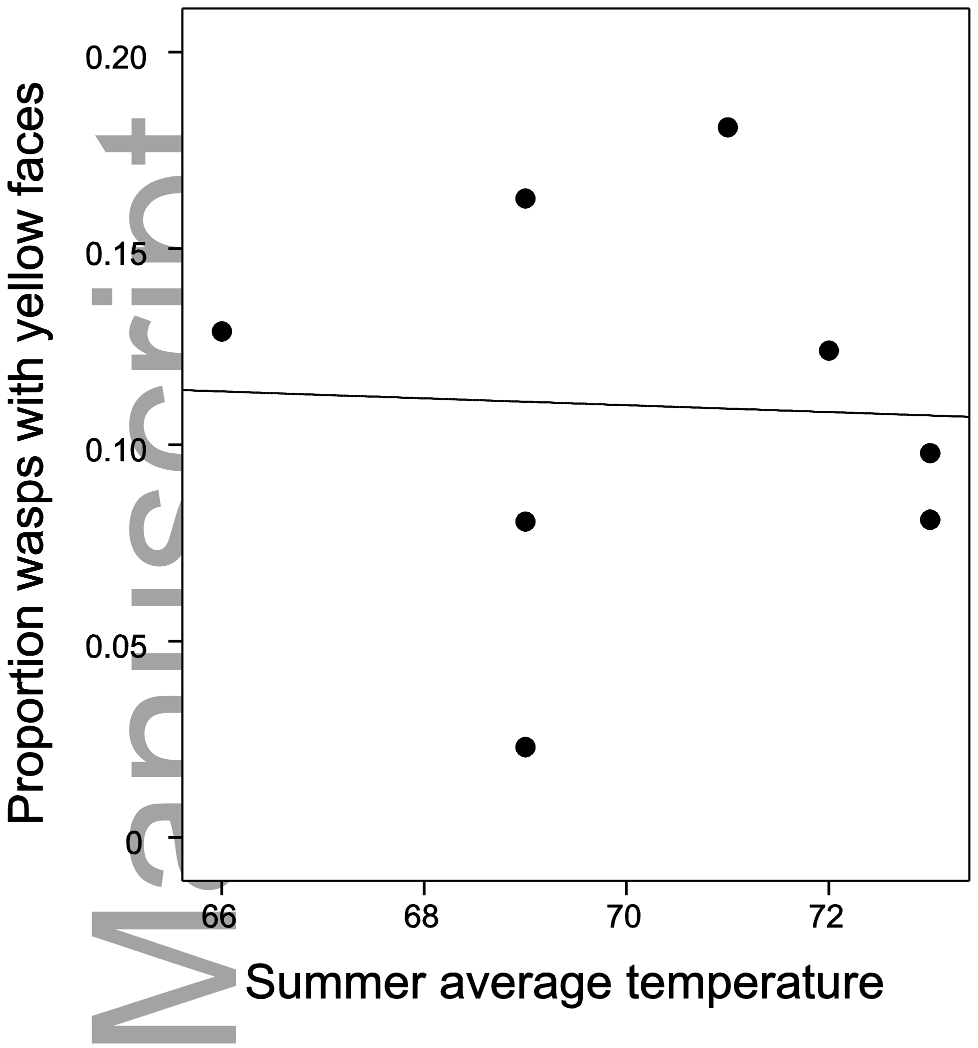
Figure 3, Relationship between proportion of foundresses in the population with the entirely yellow faces that signal low fighting ability and a) winter and b) summer temperature (in Fahrenheit).

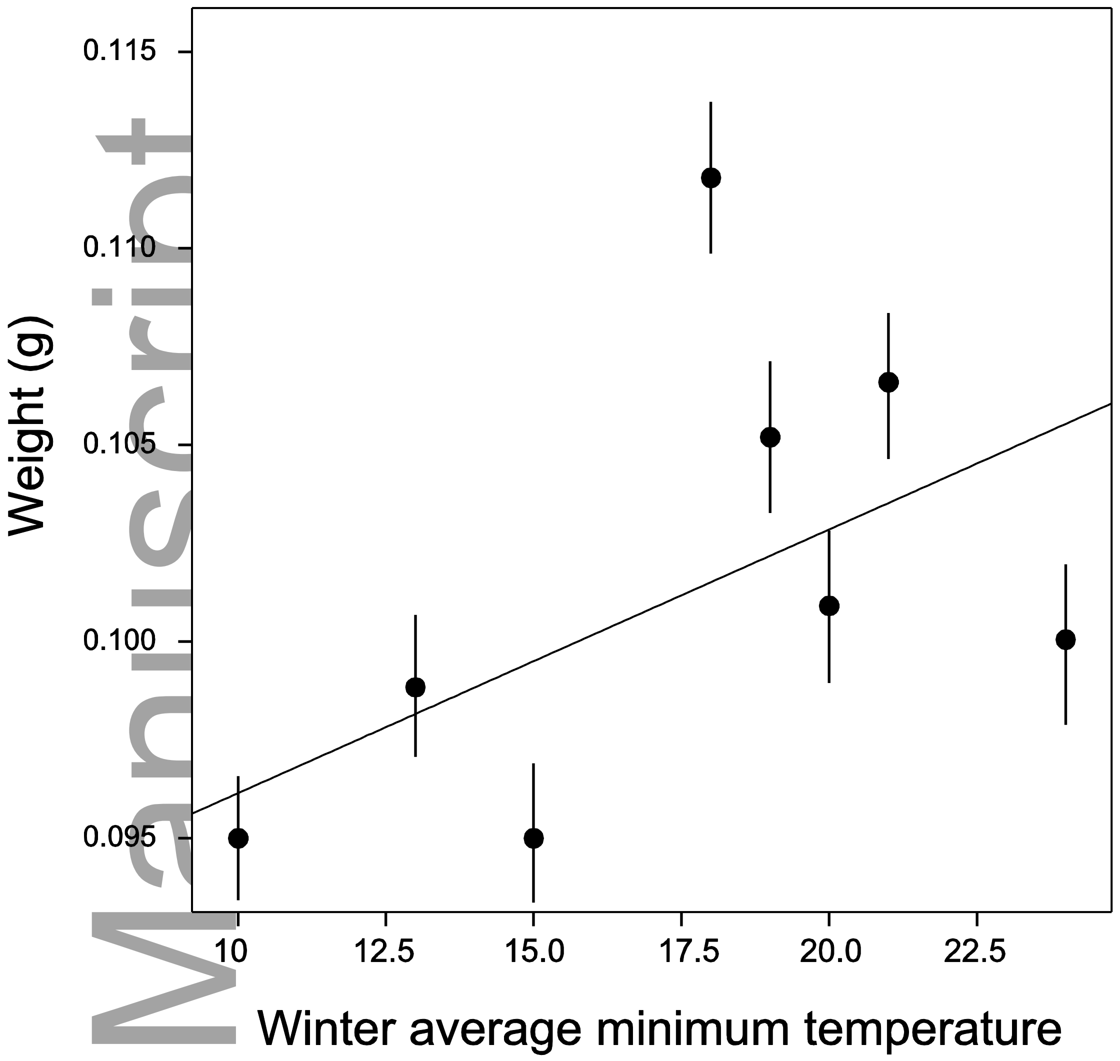
Figure 4, Relationship between average foundress weight and a) winter and b) summer temperature (Fahrenheit). Error bars are ± SE

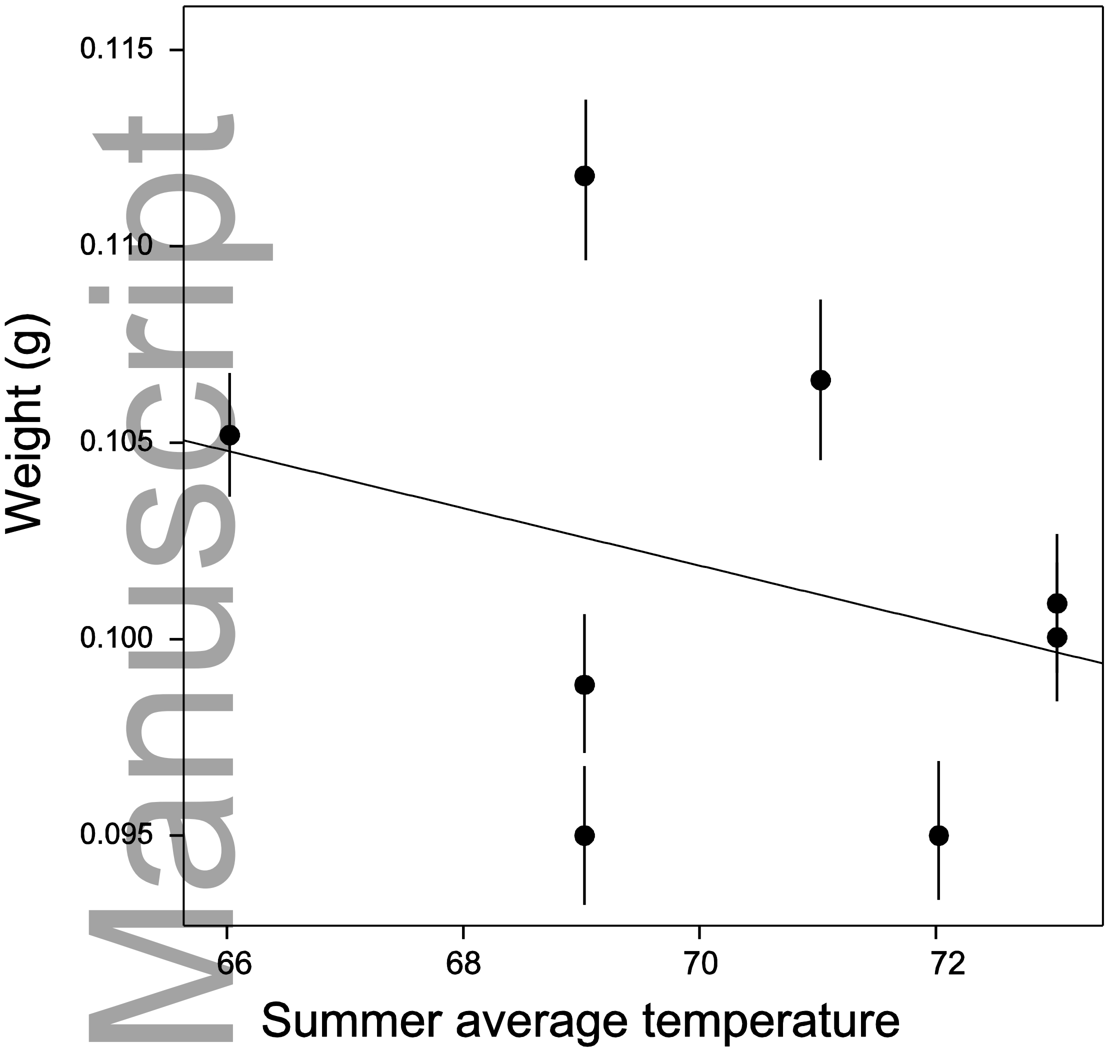
Figure 5, Mean ± SE a) facial pattern brokenness and b) weight of wasps that obtain ranks 1-4 in wild cofoundress associations. Dominant wasps had higher facial pattern brokenness and were larger than subordinate wasps


Single foundress nests
Number of nest cells
0
50
100
150
200
250
0
0.2
0.4
0.6
0.8
1.0
Facial pattern brokenness


Multiple foundress nests
Number of nest cells
0
50
100
150
200
250
0
0.2
0.4
0.6
0.8
1.0
Facial pattern brokenness

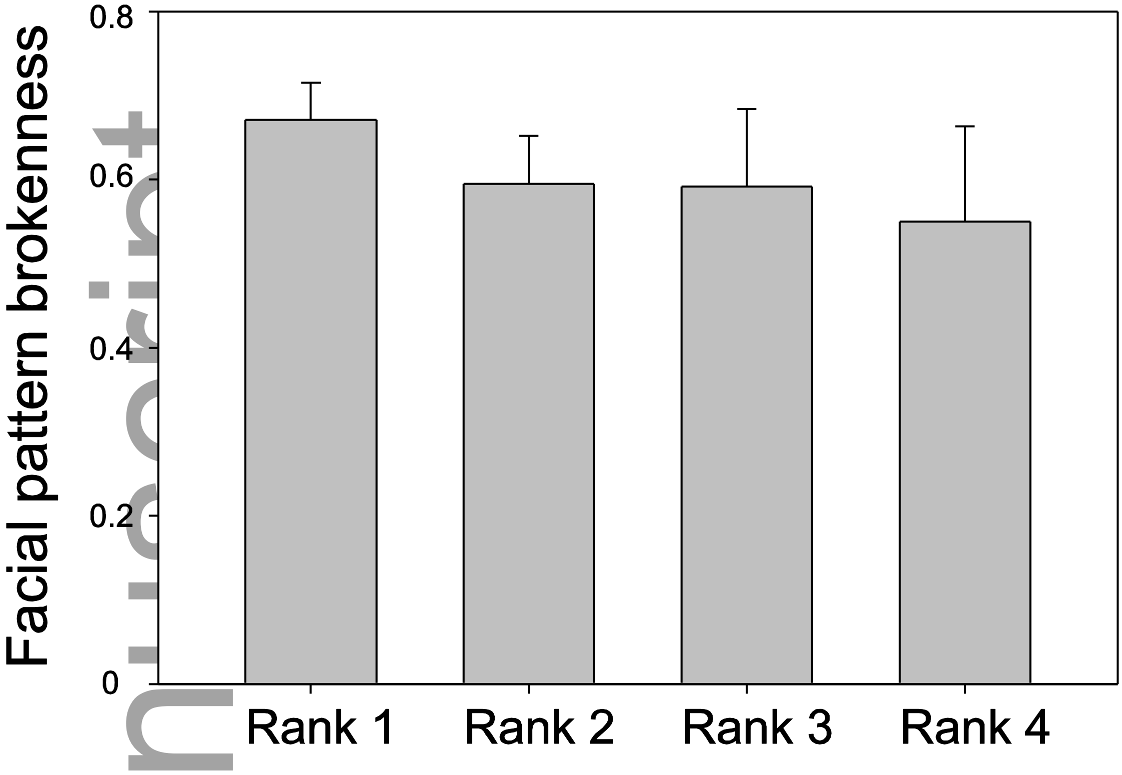

Proportion wasps with yellow faces
0.20
0.15
0.10
0.05
0
66
68
70
72
Summer average temperature

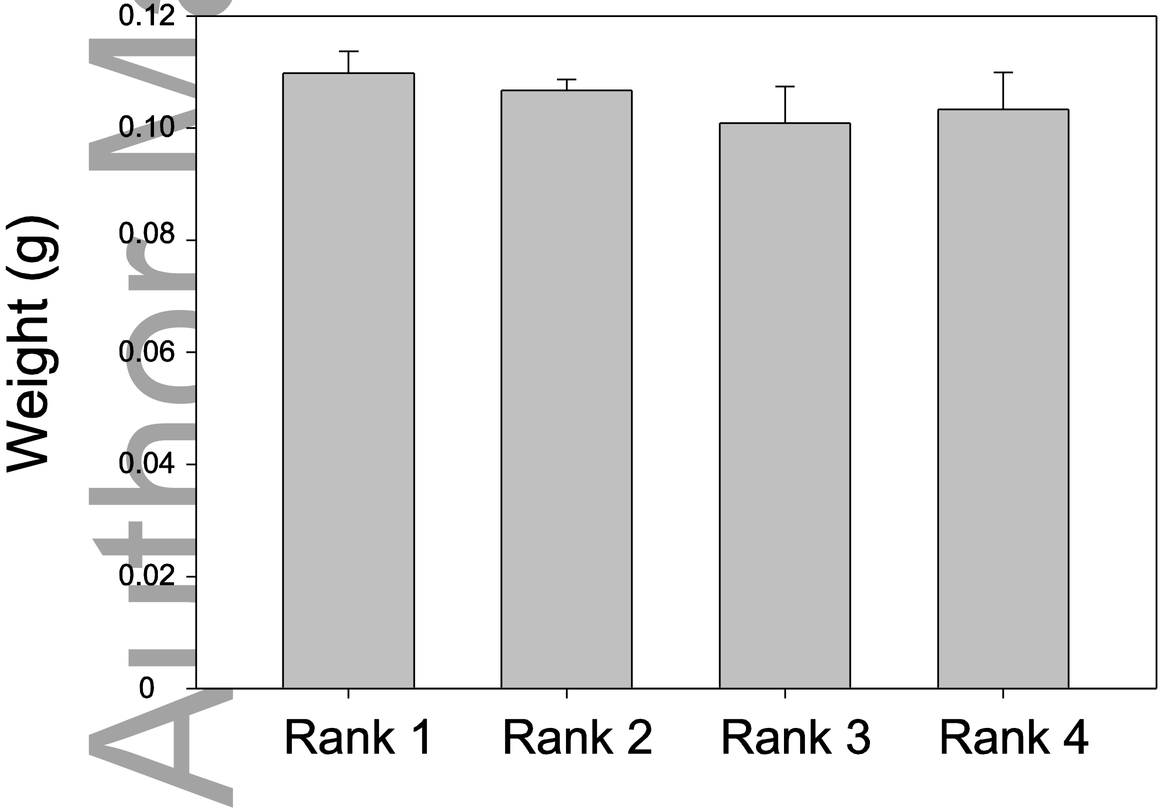

0.115
0.110
0.105
0.100
0.095
Weight (g)
10
12.5
15.0
17.5
20.0
22.5
Winter average minimum temperature

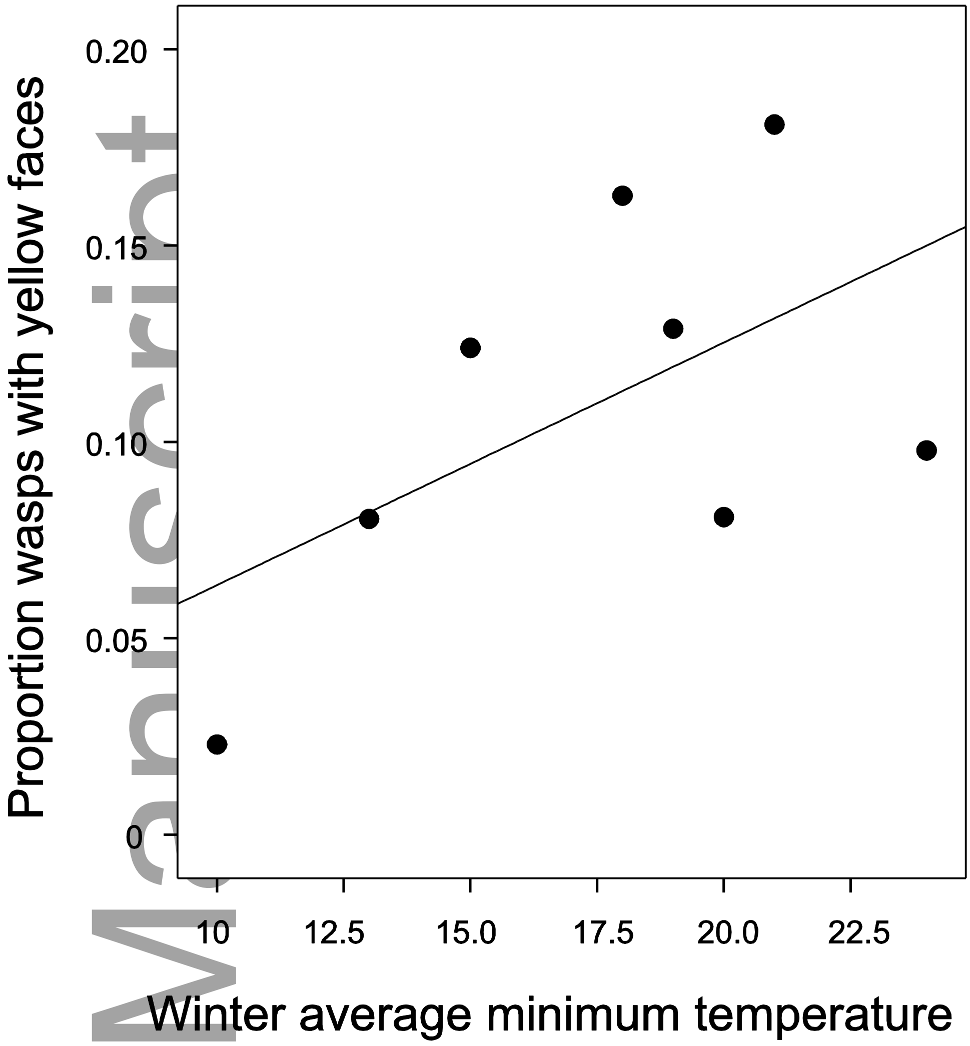

0.115
0.110
0.105
0.100
0.095
Weight (g)
66
68
70
72
Summer average temperature

551

552


Facial pattern brokenness
0
0.2
0.4
0.6
0.8
Rank 1
Rank 2
Rank 3
Rank 4


Weight (g)
0
0.02
0.04
0.06
0.08
0.10
0.12
Rank 1
Rank 2
Rank 3
Rank 4



	F	p	η^2
Facial pattern brokenness	$F_{1,605}=13.1$	$p<0.0001$	$\eta^2=0.021$
Single or multiple foundress	$F_{1,605}=73.9$	$p<0.0001$	$\eta^2=0.11$
Time of season	$F_{1,605}=120.7$	$p<0.001$	$\eta^2=0.17$
Year	$F_{1,605}=14.2$	$p<0.0001$	$\eta^2=0.023$
Body weight	$F_{1,605}=0.41$	$p=0.52$	$\eta^2=0.001$

Table 1. Results of a general linear model analyzing the factors associated with nest size.