

LETTER

Different axes of environmental variation explain the presence vs. extent of cooperative nest founding associations in *Polistes* paper wasps

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Abstract

Ecological constraints on independent breeding are recognised as major drivers of cooperative breeding across diverse lineages. How the prevalence and degree of cooperative breeding relates to ecological variation remains unresolved. Using a large data set of cooperative nesting in *Polistes* wasps we demonstrate that different aspects of cooperative breeding are likely to be driven by different aspects of climate. Whether or not a species forms cooperative groups is associated with greater short-term temperature fluctuations. In contrast, the number of cooperative foundresses increases in more benign environments with warmer, wetter conditions. The same data set reveals that intraspecific responses to climate variation do not mirror genus-wide trends and instead are highly heterogeneous among species. Collectively these data suggest that the ecological drivers that lead to the origin or loss of cooperation are different from those that influence the extent of its expression within populations.

Keywords

Bet hedging, climate predictability, ecological constraints, group size, helping behaviour, reproductive skew, social evolution, social insects, thermoregulation.

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INTRODUCTION

Although the importance of relatedness in shaping patterns of cooperation has recently been debated (Nowak *et al.* 2010; Liao *et al.* 2015), there is broad theoretical and empirical consensus that ecological constraints on independent breeding can favour cooperation (Brockmann 1997; Hatchwell & Komdeur 2000; Nowak *et al.* 2010; Jetz & Rubenstein 2011; Purcell 2011). Comparative and field studies have documented diverse ecological constraints on independent breeding including habitat saturation (Komdeur 1992), harsh foraging conditions (Faulkes *et al.* 1997), predation (Strassmann *et al.* 1988) and parasitism (Feeney *et al.* 2013). Despite several early comparative studies comparing cooperation and environmental factors (Reeve 1991; Faulkes *et al.* 1997; Arnold & Owens 1999), the nature of the environmental constraints that favour cooperative breeding and the extent of their influence across lineages remain largely unresolved.

There has been renewed interest in recent years in using phylogenetic comparative methods and global climate data sets to identify aspects of environmental variation that are associated with cooperative breeding (e.g. Jetz & Rubenstein 2011; Gon-

zalez *et al.* 2013). However, two major critiques of comparative studies of cooperative breeding have emerged. First, comparative analyses of cooperative breeding tend to rely on binary classifications of social systems, while ignoring the variation in the intensity of cooperation among taxa (Ligon & Burt 2004; Cockburn 2013). Second, macroevolutionary patterns in some groups contradict findings from many population-level studies, complicating the interpretation of results (Cockburn & Russell 2011; Cockburn 2013). At the heart of both critiques is our ability to distinguish which environmental factors are associated with the presence vs. extent of cooperative breeding. Categorical classification systems may reveal which environmental factors are associated with the presence of cooperative strategies, but only data comparing the degree of cooperation across taxa can provide insights into what factors shape the extent of cooperation among lineages.

There are at least two alternative views on the role that environmental factors play on the occurrence and intensity of cooperative breeding. One view argues for cooperation being considered as a continuum (Sherman *et al.* 1995; Avilés & Harwood 2012). Under such a scenario, elevated values of a particular environmental feature might be associated with

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cooperation and the most cooperative species are expected to occupy ranges with the most extreme environmental values. Changes in cooperation levels in this scenario are also expected to be associated with the tightening or relaxation of environmental constraints. Under such a model, cooperative breeding is expected to evolve as a continuum, such that a shift from singular breeding to breeding in groups of two should not be fundamentally different from a shift going from two to three and even further increases thereafter (Sherman *et al.* 1995). If cooperation is a continuum, we may also expect the environmental features that shape macroevolutionary patterns to explain intraspecific patterns of variation in cooperative breeding as well (Cockburn 2013).

Alternatively, several authors have argued that non-cooperative and cooperative breeding systems represent shifts between qualitatively distinct social regimes (Brown 1987; Wcislo & Tierney 2009), and that the factors influencing whether or not a species cooperates are likely to differ from those that shape the proportion of the population that pursue a helping strategy (West *et al.* 2007). This hypothesis predicts that the presence of cooperation should be favoured on one side of an environmental threshold and that the rates of helping among cooperative species are not necessarily driven by the same environmental factors.

Whether variation in cooperative breeding among species is best explained by a continuous or a threshold model has important implications for understanding the evolution of cooperation. The major challenge in distinguishing between these alternatives has been a lack of quantitative estimates of variation in rates of cooperation across species as the few data available on social systems tend to be coarse-grained, and potentially arbitrarily categorised (Cockburn 2013). High-resolution data sets that provide quantitative estimates of the extent of cooperation across species are sorely needed.

To test the relationship between climate and cooperative breeding in *Polistes* paper wasps, a model genus in sociobiology (Jandt *et al.* 2014), we constructed a data set of nesting behaviour for over 30,000 wasps from 51 species (Table S1). Paper wasp colonies are initiated by adult females, known as foundresses or queens (Reeve 1991). In temperate habitats, colony foundation occurs in the spring, after adult wasps emerge from winter diapause. Colony foundation is more asynchronous in the tropics (Reeve 1991). While *Polistes* wasps are eusocial (i.e. there are queens and workers), there is marked variation across species in the extent to which new nests are founded by solitary foundresses (non-cooperative) or associations of multiple foundresses (cooperative) (Fig. 1). Thus, species appear to differ in the extent to which foundresses seek to join established nests, accept potential cooperators or some combination of those two. Within cooperative associations, foundresses engage in dominance contests with the most dominant foundress assuming the role of the primary egg layer, whereas lower ranking individuals engage in more foraging and less reproduction (Jandt *et al.* 2014). Thus, *Polistes* foundress associations present a classic example of cooperative breeding with skewed reproduction among nest members (Reeve *et al.* 2000; Seppa *et al.* 2002; Leadbeater *et al.* 2011).

In this study, we set out to answer three fundamental questions regarding the relationship between climate and coopera-

tive nesting in *Polistes*. First, what aspects of climate are associated with the presence or absence of cooperative nesting? Second, are these same climatic features associated with the extent of cooperation among species? Third, to what extent do climatically driven patterns of variation in cooperative nesting within species match patterns of variation among species within a genus?

METHODS

Data on cooperative behaviour

We collected information on cooperative behaviour from published data on wasp nesting, our own unpublished field records, and data from online natural history databases including Bugguide (<http://bugguide.net>) the Atlas of Australia (<http://www.ala.org.au>) and iNaturalist (www.inaturalist.org) of foundress associations in wasps. The uncovered nests of *Polistes* wasps allow for the easy determination of the stage of colony progression, even from photographs (Fig. 1). As a general rule, published accounts of wasp nests (and our own field data) report counts made during the early morning or late evening, when all foundresses are present and quantifying the number of wasps on a nest is straightforward. However, because the number of foundresses observed at a nest can fluctuate over the course of colony development and throughout the day, the numbers reported here should be seen as estimates rather than the 'true' numbers of foundresses per species (West Eberhard 1969). Because we were interested in the number of foundresses that associate in the formation of colonies, we included observations of colonies during the pre-emergence phase of the colony cycle during which only foundresses are present (West Eberhard 1969; Reeve 1991). If observations of the pre-emergence phase nests were not available we used records of the number of foundresses present on nests as determined by dissection of ovarian development or the number of foundresses that contributed to the brood via genetic analysis. Indirect measures of foundress number (i.e. photographs and ovarian counts) constituted only 1.17% (101/8613) of the nests observed in *Polistes* in our data set (Supplemental Text).

Analysing the present data set requires a balance between including data on more species and stringent filtering for data quality. We strike a balance between inclusivity and data quality by conducting two separate analyses. In the first analysis we use all the data available and report aggregate values for each species (hereafter referred to as the 'aggregate' analysis). The aggregate data set has the benefit of including as many species as possible, though estimates of the size of cooperative nesting groups are based on small numbers of foundresses in some cases (Table S1). In the second analysis, we stringently filtered the data by only considering well-sampled localities for each species (hereafter referred to as the 'locality' analysis). The locality analysis includes fewer species and phylogenetic contrasts, but the continuous estimates are robust as they are based on the behaviour of many foundresses from the same location (Supplemental Text).

In the aggregate data set, we made use of all available data for each species to estimate rates of cooperation, aggregating



Figure 1 Polistine wasp nests are initiated by single foundress or groups of foundresses. The open-structure of the nest makes determination of group size and colony stage straightforward. Species shown left to right are *P. fuscatus*, *P. annularis* and *P. bahamensis* (Photos by M.J. Sheehan).

nest observation data from all sources (Table S1). We use the aggregate data set (Table S1) for three analyses: (1) the distribution of rates of cooperation across species, (2) ancestral state reconstructions, and (3) comparative analyses of the relationship between cooperation and climate. In addition to continuous estimates of the average size of cooperative foundress associations, we also categorised species as either ‘cooperative’ or ‘non-cooperative’ based on categorisations used in the literature. We note that the continuous estimates of cooperation are in agreement with traditional descriptive categories.

In the locality data set (Table S2), we made an attempt to define localities as narrowly as possible, to the level of municipality, using the verbal descriptions or specific place names of sampling in each study. Although some variation in climate can be expected within large metropolitan areas or municipalities, it is unlikely that characterising the climate variables of such localities from a single georeference will bias our results because variation in precipitation and temperature at a local scale is minimal in comparison to the regional differences observed between distant localities from the same or different species. We were conservative in our locality data set and only considered localities where the nesting behaviour of at least 20 foundresses from a given species had been observed ($N = 129$ localities across 28 species, range 1–22 localities per species, Table S2).

For both the aggregate and locality data sets, we calculated the mean number of foundresses as well as the percentage of foundresses in a subordinate role, measures that have been previously used to compare rates of cooperative nesting in *Polistes* (Hughes *et al.* 1993). We chose to measure cooperative nesting behaviour as mean number of foundresses and percent subordinates because it was possible to calculate these statistics for the largest number of records in our data set. We considered the number of foundresses observed in excess of the number of nests as subordinate foundresses because, by extension, such foundresses could not have nested solitarily and because each nest has a single most dominant female. For example if 150 foundresses were observed on a total of 100 nests, then the 50 excess foundresses were considered subordinate, meaning

that 33% of the foundresses observed in the population were subordinate. These measures are related to each other, though not in a linear manner (Fig. S1). In particular, calculating percentage of foundresses in a subordinate role places greater emphasis on variation between means of 1 and 2 foundresses (i.e. 0–50%) than between higher rates of cooperation, e.g. an increase from a mean of 2–3 foundresses corresponds to 50–66.67%. Overall, we believe that these measures reasonably capture variation in the extent of cooperation across species as they distinguish between species with nests of different foundress-association sizes.

It is important to emphasise that our measures deal with the size of cooperative foundress associations and are not measures of how reproduction is apportioned within groups. In general, multiple foundress associations in *Polistes* wasps show evidence of reproductive skew among foundress, though the extent of skew is highly variable even within populations (Reeve *et al.* 2000; Seppa *et al.* 2002). While dominant foundresses typically enjoy a disproportionate share of reproduction within multiple foundress associations, they are not the sole breeders; subordinate reproduction is commonly reported in *Polistes* (Reeve *et al.* 2000; Seppa *et al.* 2002). Regardless of the amount of skew, multiple foundress associations are cooperative in the sense that foundresses provide care to offspring that are not their own (West Eberhard 1969; Reeve 1991; Jandt *et al.* 2014).

Phylogenetic reconstruction

Phylogenetic reconstruction was performed on 71 taxa, 17 out-group species in the genera *Apoica*, *Mischocyttarus*, *Polybia*, *Protopolybia* and *Ropalidia* and 54 *Polistes* taxa, using sequences from two mitochondrial loci. All sequence data were taken from GenBank (Table S3). A 563 base pair portion of the 16S ribosomal RNA gene was used for all taxa except ten, *P. apachus*, *P. carnifex*, *P. biglumis*, *P. olivaceus*, *P. erythrocephalus*, *P. satan*, *P. instabilis*, *P. versicolor*, *M. immarginatus*, *M. mexicanus* and *R. fasciata*, for which only 350 or fewer bases were available. In addition, a 1234 base pair portion of the cytochrome oxidase subunit I (COI) gene was

used. For COI sequences 56 taxa had at least 75% shared sequence length included, however, only 376–658 bases were available for 19 of the taxa. Sequences for each gene were aligned separately using ClustalW (Thompson *et al.*, 1994) and manually adjusted for accuracy. These alignments were then concatenated and used for Bayesian analyses in MRBAYES v3.1.2 (Huelsenbeck and Ronquist, 2001). Two runs of four parallel Markov chain Monte Carlo chains under the GTR + I + Γ model were performed for 800 000 generations, sampling every 1000 generations, at which point the standard deviation of split frequencies was effectively zero. From each analysis a 50% majority rule consensus tree was produced from 1000 samples with a 25% burn-in of trees. Multiple polytomies with low support were recovered in the analysis. However, the overall topology of the tree is very similar to that resolved previously using morphological data (Pickett & Carpenter 2010), suggesting that the low support values stem from a need for more informative sequence data rather than inaccurate tree reconstruction. A full version of the phylogeny is shown in Fig. S2.

Ancestral state and area reconstruction

We reconstructed the evolutionary history of cooperative nesting in *Polistes* using the parsimony reconstruction model of continuous data in Mesquite v 2.75 (Maddison & Maddison 2003) using the mean number of foundresses and percent of subordinate foundresses as a continuous measures respectively. In addition, we considered the evolution of cooperative breeding as a categorical variable, using the likelihood reconstruction model for categorical data in Mesquite v 2.75. We ran the analyses using the previously constructed Bayesian tree pruned to 47 species for which we had data on social systems: 40 species of *Polistes* and five species of *Mischocyttarus*, one species of *Belonogaster* and one species of *Ropalidia* as outgroups.

We reconstructed the evolution of geographical ranges in *Polistes* and its relatives using the maximum likelihood dispersal-extinction-cladogenesis model as implemented in “Lagrange” (Ree & Smith 2008). We employed a temporally unconstrained model in which dispersal probabilities between regions were assumed to be symmetric.

The following six biogeographical regions were used in the analysis: (1) Neotropics (South America, Central America and the Caribbean), (2) the Nearctic (North America); (3) the Western Palearctic (Europe, Central Asia, Middle East and North Africa); (4) the Eastern Palearctic (temperate East Asia); (5) Indo-Malaya and Oceania (South Asia, Peninsular and Insular Southeast Asia, New Guinea and Australia); and (6) the Afrotropics (Sub-Saharan Africa). See the supplemental methods for further justification of the choice of regions. We calculated a geographical reconstruction pertaining to one fully dichotomous phylogeny randomly resolved from the multichotomous tree using the R package ‘picante’ (Fig. S3, Kembel *et al.* 2010).

Climate analysis

We used a total of 4103 georeferenced observations of species from museum specimens (GBIF: <http://www.gbif.org>), field

observations (Bugguide: <http://bugguide.net>; Atlas of Australia: <http://www.ala.org.au>) and localities described in the published literature on each species (median number of records = 58, range: 4–1108). For each record of each species we extracted 13 variables capturing the mean, variance and predictability of temperature, precipitation and primary productivity variables from Bioclim and the CRU-TS 3.1 Climate Database (Mitchell & Jones 2005; see Table S4 for further information on the variables considered). Predictability of climate variables was measured as Colwell’s P (Colwell 1974), which takes into account both the contingency and constancy of climate patterns between years. The aggregate species mean for each of the variables was calculated and a principal component analysis performed on the 40 *Polistes* species used in the comparative analyses. The first two principal components explained approximately 75% of the variation in the aggregate data set and can be interpreted as corresponding to variation in environmental harshness (PC1, 57% of the variance) and short-term temperature stability (PC2, 17% of the variance) (Supplemental Text, Fig. S4a). For PC1, higher values are associated with lower mean temperatures and rainfall with lower values associated with warmer, wetter conditions. High values of PC2 are associated with low differences between the high and low temperatures within a month and lower values have higher amplitude short-term temperature fluctuations. We ran an additional PCA analysis with the climate data limited to georeference points used in our locality data set (Table S2). The results of this analysis are similar to those found for the aggregate data set climate PCA (Fig. S4b): the first two principal components explain approximately 66% of the variation and correspond roughly to the same environmental features as those captured in the aggregate species PCA. That is, environmental harshness or PC1 captured 47% of the variance, and short-term temperature fluctuation or PC2 captured 20% of the variance. Indeed, the loadings on PC1 for both the species-level and population-level data sets are nearly identical (linear regression, $r^2 = 0.95$, $B = 1.01$, $P < 0.0001$) and the loadings on PC2 are very similar (linear regression, $r^2 = 0.71$, $B = 0.79$, $P = 0.0003$), reflecting the fact that both of these analyses ultimately have similarly balanced global coverage. Loading of the variables on different PC axes can be found in Table S5. Although the PC axes in both cases are not exact replicas, the high level of similarity allows for reasonably direct comparisons between the inclusive aggregate and more stringently filtered locality data sets (Fig. S5).

Four temperate species – *P. dominula*, *P. exclamans*, *P. fuscatus* and *P. metricus* – were sampled at a sufficiently large and geographically disparate set of localities to allow us to investigate intraspecific relationships between climate and cooperative nesting. Using subsets of the locality data set for each species, we modelled the mean number of foundresses observed in a given locality as a function of environmental factors.

Comparative analyses

We examined the relationships between the principal components of climate variation and our different measures of cooperation. First, we examined both PC axes as predictors

of cooperation coded as a categorical variable (cooperative vs. non-cooperative). Next, we considered both PC axes as predictors of continuous measures of cooperative nesting (i.e. mean number of foundresses and the percent of subordinate foundresses). We next examined the effects of both climate axes on continuous variation in cooperation in a reduced data set including only the cooperative species. Species were categorised as either cooperative or non-cooperative based on traditional categorisations and descriptions of the species in the literature. We examined the relationship between climate and cooperative breeding with Bayesian phylogenetic mixed models using the package MCMCglmm in R (Hadfield 2010) with flat non-informative priors, 600 000 iterations, a burnin of 200 000 and a thinning interval of 100 iterations used in all analyses. Visual inspection of the MCMC chain demonstrated convergence in all cases. In addition, we analysed our data using phylogenetic generalised least squares analyses using the R package Caper (Orme *et al.* 2012) to ascertain their robustness to different modelling procedures. For each analysis we pruned the overall phylogenetic tree (Fig. S2) to taxa for which we had data. In the locality analysis, species observed at multiple localities were represented by a polytomy with multiple tips.

RESULTS

Distribution and evolutionary history of cooperative breeding

The average number of foundresses observed on pre-emergence nests in *Polistes* species ranges from 1 to 7.5, showing a positive skewed distribution (Fig. 2a, skewness = 1.19). The percent of subordinate foundresses varies from 0 to 87% across species and shows a strongly bimodal distribution. (Fig. 2b, Hartigan's dip test, $D = 0.098$, $P = 0.0004$, $N = 51$ species). Removing poorly sampled species (< 15 foundresses observed) does not alter this result (Hartigan's dip test, $D = 0.10$, $P = 0.0003$, $N = 40$ species). Notably, the species on either side of the break in the distribution (greater or less than 10% subordinates) have historically been categorised as non-cooperative and cooperative, suggesting that these categorical descriptors may capture a biologically relevant break in patterns of cooperative nesting.

Ancestral state reconstruction indicates that cooperative nest founding has been evolutionarily labile. There is broad agreement across reconstructions using mean number of foundresses, percent subordinate foundresses and categorical measures (Figs 2c and S6). Cooperative breeding has been lost multiple independent times in *Polistes*, with increased rates of cooperation seen in some lineages (Fig. 2c). At least three independent losses of cooperative nesting in *Polistes* involve species or clades that have independently invaded eastern Asia (Figs 2c–d and S3). In addition, species with the highest rates of cooperation are found in the Neotropics (Fig. 2d). The clustering of non-cooperative and highly cooperative species in different geographical regions suggests that climatic factors may have played a role in the evolution of cooperative nesting behaviour in this genus.

Climatic correlates of cooperative breeding across species

Different aspects of climate variation are correlated with the formation vs. the size of cooperative foundress associations in *Polistes*. Table 1 shows the output for models of categorical and continuous measures of cooperation with the first two PC axes, environmental harshness and short-term temperature stability as main effects. Categorical models using both the aggregate and locality data sets show that non-cooperative species occur in regions with greater short-term temperature stability (Fig. 3). Conversely, cooperative nesting is associated with higher amplitude fluctuations in temperature. Continuous models show that the size of cooperative nesting associations is inversely related to environmental harshness, with higher rates of cooperative nesting occurring in more benign regions, i.e. the tropics (Fig. 3). Notably, environmental harshness is a better predictor of rates of cooperation when non-cooperative species are excluded from both the aggregate and locality data sets (Table 1). The overall pattern of results is equivalent whether we measure cooperation as the mean number of foundresses (Table 1) or the percentage of subordinate foundresses (Supplemental Text, Table S6).

Categorical analyses are a better fit to the aggregate data set whereas continuous analyses are a better fit to the locality data set. A model that considers short-term temperature stability as the sole predictor of categorical cooperation data is a substantially better fit in the aggregate (PGLS, $F_{2,38} = 25.63$, $r^2 = 0.39$, $P < 0.0001$) compared to the locality data set (PGLS, $F_{2,127} = 6.96$, $r^2 = 0.04$, $P = 0.009$). For the continuous data, a model that considers solely environmental harshness as a predictor of the extent of cooperation in cooperative species within the locality data set fits better (PGLS, $F_{2,84} = 34.55$, $r^2 = 0.28$, $P < 0.0001$) than its equivalent model with the cooperative only aggregate data set (PGLS, $F_{2,24} = 4.57$, $r^2 = 0.13$, $P = 0.021$).

Climatic correlates of cooperation within species

Global axes of climate variation that explain patterns of cooperative nesting across the genus are relatively poor predictors of variation in cooperative nesting within individual species. In the genus-wide analysis of the locality data set environmental harshness correlates with variation in the extent of cooperative nesting (Fig. 3c). However, short-term temperature stability tends to better explain variation in the size of cooperative nesting associations within the four species examined here (Fig. 4a–b, Table 2). In both *P. dominula* and *P. exclamans*, short-term temperature stability tends to be negatively associated with the mean number of foundresses. In contrast, in *P. fuscatus* short-term temperature stability tends to be positively associated with cooperative nesting. Neither of the genus-wide climate PCs explained variation in cooperative nesting in *P. metricus*. The same pattern of results is found when analysing variation in the percent subordinate foundresses for *P. exclamans*, *P. fuscatus* and *P. metricus* (Table 2). For *P. dominula*, however, the percentage of subordinate foundresses is associated with environmental harshness rather than short-term temperature stability. This difference

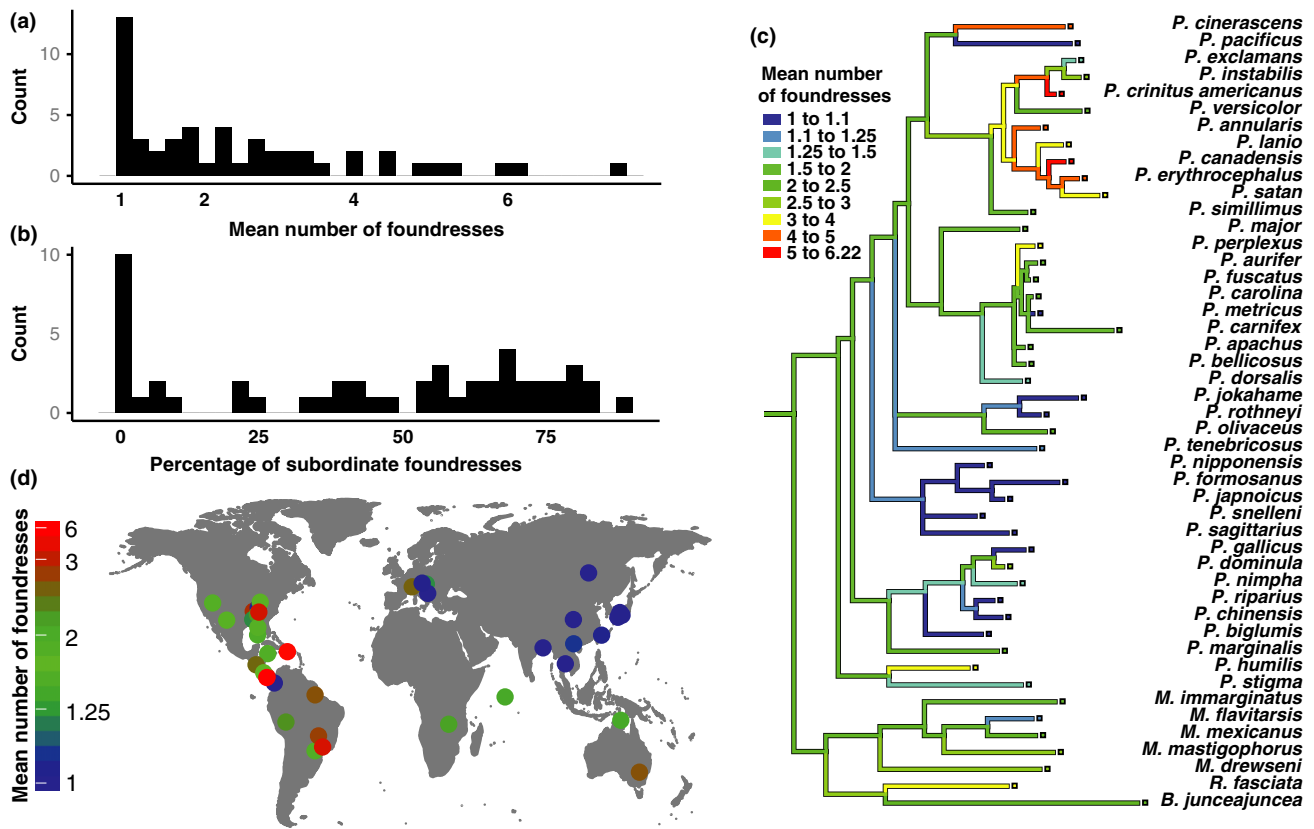


Figure 2 (a) The mean number of foundresses shows a leptokurtotic distribution across *Polistes* species. (b) Rates of cooperation measured as the percent of subordinate foundresses are bimodally distributed among *Polistes* paper wasp species. (c) Phylogeny of *Polistes* wasps with rates of cooperative nesting mapped onto the tree. Rates of cooperation have been evolutionary labile, with multiple independent losses of cooperative breeding. (d) Range centres for species examined in our cooperation data set. The dots each represent the average latitude and longitude for each species examined, with the colour denoting the level of cooperation observed in that species. Non-cooperative species are clustered in eastern Asia, whereas the most cooperative species are found in the Neotropics.

arises because mean foundress number and percent subordinate foundresses differentially emphasise variation among populations showing high or low rates of cooperative nesting respectively (Fig. S1).

Genus-wide PC axes are derived from a global data set of localities, and although they are relevant axes of climate variation at a global scale, they may not accurately reflect patterns of climatic variation within the range of single species. For example the environmental factors that explain broad patterns of variation in cooperation between temperate and tropical zones or between rainforests and deserts may be highly uninformative when it comes to the variation in cooperation observed within a species that is only present in temperate deciduous forests. Thus, we conducted a second-set of intraspecific analyses where we calculated climate PCs specific to the population data sets for each species. As expected from the limited distributions of the focal species, species-specific climate PCs differ considerably from genus-wide PCs (Fig. S7). Analyses of patterns of variation in cooperative nesting relative to species-specific climate PCs reveals considerable heterogeneity among species (Table S7) – in *P. dominula* cooperation is positively associated with warmer, predictable temperature regimes (Fig. S8a, $F_{1,17} = 10.78$,

$r^2 = 0.35$, $P = 0.004$); in *P. fuscatus* cooperation is higher with more predictable precipitation patterns (Fig. S8b, $F_{1,18} = 6.60$, $r^2 = 0.23$, $P = 0.019$); in *P. metricus* cooperation is highest with less predictable precipitation patterns (Fig. S8c, $F_{1,20} = 7.27$, $r^2 = 0.23$, $P = 0.014$); in *P. exclamans* neither of the first two principal components explain variation in cooperation rates (Fig. S8d).

DISCUSSION

Our results demonstrate that the axes of global environmental variation associated with shifts between cooperative and singular nesting are different from those that explain variation in the size of cooperative nesting associations across species. Put simply, the environmental pressures associated with increasing from one to two foundresses do not explain the increase from two to three foundresses. We find the same pattern of results using both a comprehensive, though noisy data set of aggregate measures for all species and a stringently filtered data set based solely on well-sampled localities, demonstrating that our findings are robust. Our results therefore suggest that being willing or able to form any cooperative nesting association is a fundamental step in social evolution. Notably, the

Table 1 Comparative results

Cooperation measure	Climate PC axis	Bayesian			PGLS		
		Posterior mean	95% CI Bounds	pMCMC	<i>t</i>	<i>P</i>	<i>r</i> ²
All aggregate data (<i>N</i> = 40 species)							
Categorical	Env. Harshness	-8.68	-56.92-38.17	0.72	-0.28	0.78	0.37
	Temp. Stability	175.66	36.69-318.94	0.0013	-5.00	< 0.0001	
Mean	Env. Harshness	-0.112	-0.30-0.065	0.21	-1.19	0.24	0.02
	Temp. Stability	-0.191	-0.52-0.15	0.26	-1.11	0.28	
Cooperative species only aggregate data (<i>N</i> = 26 species)							
Mean	Env. Harshness	-0.186	-0.435-0.065	0.12	-1.89	0.07	0.09
	Temp. Stability	0.090	-0.51-0.72	0.77	0.41	0.69	
All locality data (<i>N</i> = 129 localities, 28 species)							
Categorical	Env. Harshness	-7.76	-62.85-49.87	0.81	1.37	0.17	0.05
	Temp. Stability	58.06	-2.10-136.13	0.041	-2.68	0.008	
Mean	Env. Harshness	-0.177	-0.293 to -0.062	0.003	-2.97	0.004	0.05
	Temp. Stability	-0.032	-0.191-0.130	0.69	-0.36	0.72	
Cooperative species only locality data (<i>N</i> = 86 localities, 19 species)							
Mean	Env. Harshness	-0.262	-0.383 to -0.124	0.001	-5.91	< 0.001	0.28
	Temp. Stability	0.046	-0.172-0.256	0.66	0.81	0.41	

bimodal distribution of the rates of cooperation across species is consistent with a model where non-cooperative and cooperative breeding represent two distinct states. In other realms of ecological research, bimodal distributions have been interpreted to be driven by regime shifts in other systems as well (Scheffer *et al.* 2014) or to be indicative of bistability of ecosystems (Staver *et al.* 2011). Specifically, the bimodal distribution in rates of cooperative nesting observed in *Polistes* wasps appear to be the result of opposing selection pressures favouring either cooperative or non-cooperative strategies at either side of an environmental threshold.

The loss of cooperative nesting is associated with reduced temperature fluctuations over short time scales. Comparative studies of cooperative breeding in vertebrates have focused on the role of year-to-year environmental predictability in shaping cooperative behaviour (Faulkes *et al.* 1997; Jetz & Rubenstein 2011; Gonzalez *et al.* 2013). Compared to relatively long-lived cooperatively breeding vertebrates, paper wasps have a short lifespan with annual colony cycles (Reeve 1991; Brockmann 1997). Thus, it is perhaps less surprising that variation during the course of a wasp's life rather than between generations is more salient in this case.

A number of investigators have examined the influence of microhabitat temperature on nest site choice and colony productivity in *Polistes* (Cervo & Turillazzi 1985; Jeanne & Morgan 1992; Nadeau & Stamp 2003). However, little work has explicitly examined the influence of the amplitude of temperature fluctuations. We suggest two non-mutually exclusive routes through which short-term temperature fluctuations may influence cooperation in paper wasps. First, large diurnal and day-to-day temperature fluctuations can have negative implications for growth and development in insects (Colinet *et al.* 2015). Unlike many bees and ants, paper wasps have small, exposed nests, which offer little buffer from environmental fluctuations (Jones & Oldroyd 2006). This is especially true at the founding stage when nests are small (Hozumi & Yamane 2001). Higher amplitudes of temperature fluctuation may

represent more stressful conditions for both larval development and adult physiology given the limited thermoregulatory capacity of *Polistes* wasps (Weiner *et al.* 2010). More stressful nesting conditions, in turn, may favour cooperation. Second, fluctuating temperatures may also affect wasps by reducing the amount of time available for foraging. Wasps tend to be inactive at lower temperatures and some species have narrow temperature ranges for optimal flight (Weiner *et al.* 2012). At higher temperatures, adults forgo nutrient foraging and invest in nest-directed thermoregulatory behaviours including fanning the nest and collecting water to drench the nest for evaporative cooling (Rau 1931). Cooperation may be advantageous when there are larger amplitude temperature fluctuations as groups of foundresses may be able to more effectively take advantage of windows suitable for foraging. The current findings call for work integrating studies of thermal physiology and cooperative nesting in *Polistes* wasps to elucidate the mechanisms driving the pattern uncovered in this study.

The largest cooperative groups are not found among species with the most extreme temperature fluctuations, but rather those occupying benign climates with warm and wet conditions. At face-value this finding appears to challenge much of the work emphasising the role of ecological constraints on independent breeding in favouring cooperative breeding (Faulkes *et al.* 1997; Hatchwell & Komdeur 2000). Benign environmental conditions, however, have also been argued to potentially lead to increased rates of cooperation due to habitat saturation (Selander 1956; Arnold & Owens 1999; Gonzalez *et al.* 2013). There is some evidence of higher rates of cooperative nesting in denser *Polistes* populations (Brockmann 1997) though there is no evidence that Neotropical species with the highest rates of cooperation nest at higher density or are closer to their carrying capacity than *Polistes* in other parts of the world. Alternatively, it is possible that wasps in regions with benign abiotic conditions are faced with harsher biotic interactions. In particular, rates of ant predation on wasp larvae have been experimentally

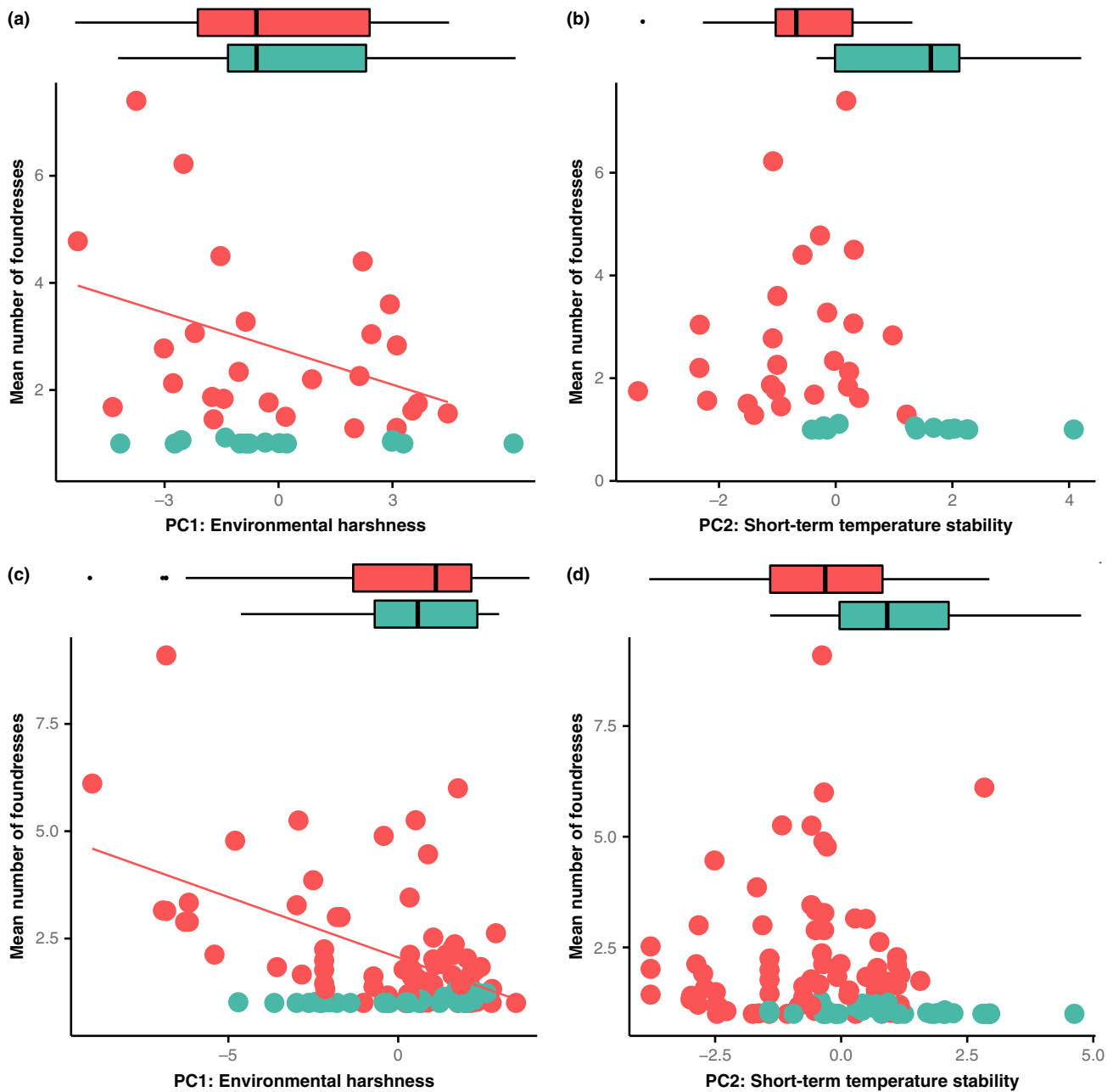


Figure 3 Similar patterns of results are found for analyses using aggregate (a–b) and locality data sets (c–d). In the aggregate data set, the climate and cooperation data are based on the aggregate of all available data for each species. For the locality data set, climate and cooperation data are specific to particular localities. In both data sets, environmental harshness PC is negatively associated with the rate of cooperative nesting among cooperative species but does not separate cooperative from non-cooperative species (a, c). Greater short-term temperature stability is associated with non-cooperative nesting species in both the aggregate and locality data sets (b, d). The scatterplots show the continuous variation in raw data for each analysis with trend lines denoting a significant phylogenetically corrected relationship. Boxplots show the distribution of climate variables for each category of species. Cooperative species are denoted with red and non-cooperative with blue.

shown to be higher in the Neotropics compared to temperate North America (Jeanne 1979), and are thought to have been a major evolutionary force shaping nest site selection in tropical Polistine wasps (Corbara *et al.* 2009). Currently, data on any moderating effects of foundress number on mitigating ant attacks is lacking. More broadly, larger foundress associations have been shown to be more resilient against vertebrate predation as well as defending against parasitoids (Strassmann 1981; Strassmann *et al.* 1988). The

Neotropics also has elevated levels of species diversity in *Polistes* and related genera (Corbara *et al.* 2009), raising the possibility that competition may be greater in the paper wasp niche in the Neotropics compared to temperate regions. Relatively little is known about the comparative population demography, predation and parasitism pressures across *Polistes* though future work in this area holds important promise for understanding patterns of cooperation across species.

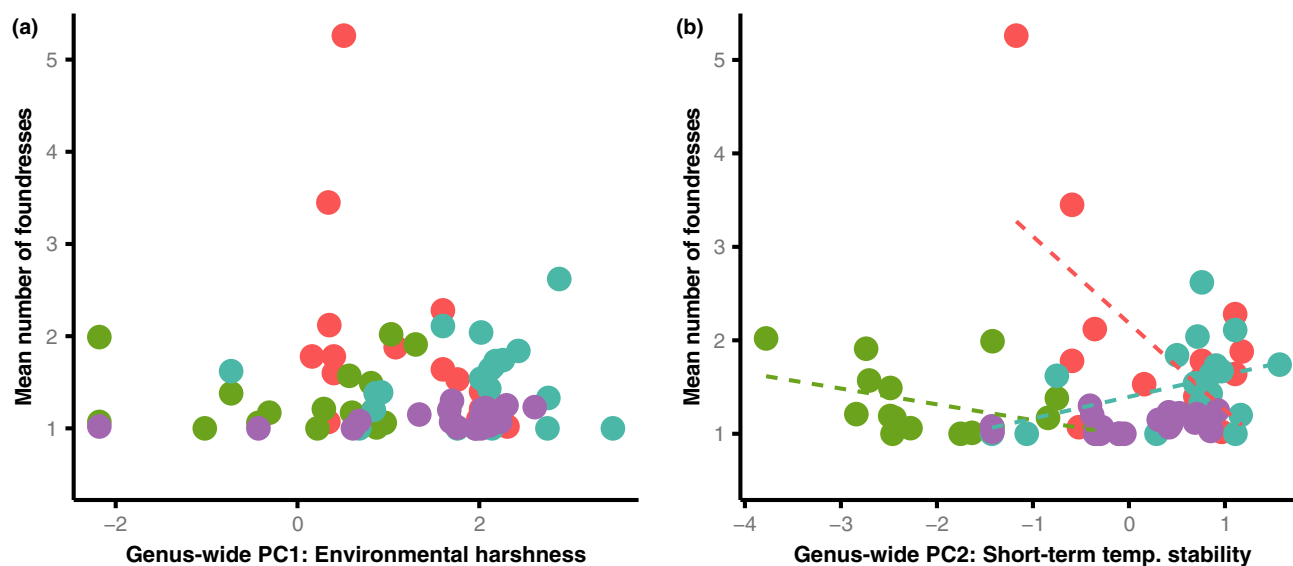


Figure 4 (a) Environmental harshness that correlates with interspecific variation in the extent of cooperation across the genus, but does not explain intraspecific variation in rates of cooperation in any of the four species examined: *P. dominula* (red), *P. fuscatus* (blue), *P. metricus* (purple) and *P. exclamans* (green). (b) Short-term temperature stability, which is associated with the presence of cooperation at the macroevolutionary scale, tends to explain variation in the extent of cooperative nesting among populations in three of the species. The trends in *P. dominula* and *P. exclamans* are in line with the genus-wide patterns though *P. fuscatus* shows an opposite response to fluctuating temperatures.

Table 2 Interspecific analyses

Genus-wide population-level climate PCs						
Species	Mean foundresses			Percent subordinate		
	<i>F</i> or <i>t</i>	<i>r</i> ²	<i>P</i>	<i>F</i> or <i>t</i>	<i>r</i> ²	<i>P</i>
<i>P. dominula</i>						
Whole model	6.07	0.36	0.010	6.24	0.37	0.010
Env. harshness	-0.62		0.54	2.3		0.036
Fluctuating temp.	-2.08		0.054	-0.39		0.71
<i>P. exclamans</i>						
Whole model	2.21	0.13	0.15	1.86	0.097	0.19
Env. harshness	-1.07		0.3	0.87		0.398
Fluctuating temp.	-2.10		0.055	-1.90		0.078
<i>P. fuscatus</i>						
Whole model	1.9	0.09	0.18	3.85	0.23	0.042
Env. harshness	-0.36		0.73	1.14		0.27
Fluctuating temp.	1.89		0.076	2.77		0.013
<i>P. metricus</i>						
Whole model	1.65	0.06	0.22	1.88	0.08	0.18
Env. harshness	0.91		0.37	-0.86		0.40
Fluctuating temp.	0.39		0.698	0.54		0.60

The axis of climate variation that explains genus-wide patterns of variation in the size of cooperative nesting associations do not explain intraspecific patterns of cooperative nesting in the four temperate species examined. This result is especially noteworthy for two reasons. Previous authors have criticised phylogenetic comparative studies of cooperative breeding because they did not match species-level patterns (Cockburn 2013), even though studies at different scales have used different climate data. In this study, the climate and cooperation data used to assess variation in each species was simply a subset of the locality data used in the genus-wide

analysis. Arguably, this result provides the clearest evidence to date that different processes shape variation in the rates of cooperation within and between species. Indeed, analyses of intraspecific variation in rates of cooperation demonstrate that variation in cooperative nesting is often associated with environmental variation, though the relevant gradients differ across species (Fig. 4). The major axes of climate variation at the global scale are rarely replicated within the range of an individual species, so it is not surprising that important features of climate variation may differ at local and global scales (Fig. S6). Notably, the species we examined shared partly overlapping ranges and still showed heterogeneous responses to climate variation suggesting that species' cooperative nesting responses to climate variation are evolutionarily labile within *Polistes* (Fig. 4). The heterogeneity in the relationships between cooperation and environmental conditions among species urges caution in extrapolating findings on the climatic drivers of cooperation from a single population or species to broader geographical and spatial scales. Thus, criticisms that the results of comparative studies examining the relationship between cooperation and the environment do not concur with intraspecific studies (Cockburn & Russell 2011; Cockburn 2013) should be re-evaluated in light of the fact that predictors of the formation of cooperative groups and size of those groups need not be the same (West *et al.* 2007, this study).

CONCLUSION

Detailed records of wasp nesting behaviour have allowed us to examine the relationships between cooperative nesting and climate using different metrics across phylogenetic and spatial scales. These analyses reveal that different aspects of climatic variation are associated with the presence and extent of

cooperation both within and across species. Interestingly, estimates of the average climate for each species are a better predictor of the presence of cooperation than climate variables from the limited subset of populations where species have been observed and vice versa for continuous measures of cooperation. This result suggests that the propensity to engage in cooperative nesting is a trait that evolves at the species-level in paper wasp while the extent of its expression (as measured by foundress group size) is potentially more plastic and dependent on local conditions. Taken together, our data provide support for variation in cooperative breeding as both an ecologically labile continuum and distinct evolutionary strategies. The disconnect between inter and intraspecific patterns of cooperative nesting in responses to climate begs for further research documenting patterns of cooperation across species' ranges, opening up a new line of questioning to understand the demographical, ecological and evolutionary processes that give rise to heterogeneity in climate responses across species.

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AUTHOR CONTRIBUTIONS

TAH performed phylogenetic analysis; MJS, JMJ, SW, ALT and EAT contributed field data on wasp nesting behaviour; MJS, CAB and BES analysed the nesting data in relation to climate; and MJS conceived and designed the study, constructed the database of cooperative nesting, and also wrote the manuscript with input from other authors.

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