



## Original Article

# Queen succession conflict in the paper wasp *Polistes dominula* is mitigated by age-based convention

Benjamin A. Taylor,<sup>a,b,e</sup> Alessandro Cini,<sup>a,b,c</sup> Rita Cervo,<sup>c</sup> Max Reuter,<sup>b</sup> and Seirian Sumner<sup>a,b</sup>

<sup>a</sup>Centre for Biodiversity and Environment Research, University College London, Gower Street, London WC1E 6BT, UK, <sup>b</sup>Department of Genetics, Evolution and Environment, University College London, Gower Street, London WC1E 6BT, UK, and <sup>c</sup>Dipartimento di Biologia, Università degli Studi di Firenze, Via Madonna del Piano 6, 50019 Sesto Fiorentino, Italy

Received 22 November 2019; revised 18 March 2020; editorial decision 14 April 2020; accepted 20 April 2020.

Reproduction in cooperative animal groups is often dominated by one or a few individuals, with the remaining group members relegated to nonreproductive helping roles. This reproductive skew can evolve if helpers receive fitness benefits such as potential future inheritance of the breeding position, but the mechanisms by which inheritance is determined are not well resolved. *Polistes* paper wasps form highly reproductively skewed groups and inheritance of the breeding position is likely to play a key role in the maintenance of this social structure, making them excellent models for the processes by which simple societies are maintained. Reproductive succession is thought to be determined via an age-based convention in some *Polistes* species, but there is also evidence for contest-based succession systems in which the replacement queen uses physical aggression to overpower and thereby subordinate her nestmates. Here, we provide evidence that queen succession in colonies of the European paper wasp *Polistes dominula* is determined via convention rather than contest, with little disruption to the colony's social functioning. We use queen removal experiments and fine-scale behavioral analyses to confirm that age is a strong predictor of succession, and that behavioral responses to queen removal are restricted to the oldest individuals rather than being experienced equally across the group. We provide the most comprehensive and detailed experimental analysis on the dynamics of breeder succession in a cooperatively breeding invertebrate to date, thereby shedding light on the mechanisms by which animal societies are able to maintain cohesion in the face of within-group conflict.

**Key words:** convention, inheritance; *Polistes*, queen replacement, reproductive conflict.

## INTRODUCTION

Group living offers substantial benefits in terms of efficiency of energy acquisition and protection against predators and parasites (Krause and Ruxton 2002; Olson et al. 2015). However, conflicts of interest between group members can threaten the cohesion of the group as a whole (Beekman et al. 2003; Ratnieks et al. 2006). Intragroup conflicts are likely to be major drivers in social evolution, and mechanisms that facilitate their resolution are predicted to be favored by selection (Rubenstein 2012; Cant and Young 2013). The mechanisms regulating the resolution of conflict in social groups have major impacts on the costs and benefits of group living, so determining these mechanisms is fundamental to achieving an understanding of the evolution of sociality. However, investigating the nature of social conflict mediation mechanisms

requires detailed data regarding individuals' behavioral and physiological responses to social disruption, which are difficult to obtain when dealing with complex societies.

Reproductive conflict is most intense in societies in which reproductive opportunities are partitioned unequally, as is the case in the cooperatively breeding groups of many birds, mammals, and social insects. A common feature of such societies is the presence of strong reproductive skew, with a relatively small number of high-ranking individuals monopolizing reproductive opportunities (Cant and English 2006; Nonacs and Hager 2011). Much research into the evolution of cooperative breeding has focused on the benefits of this social system for subordinate individuals who would appear to be disadvantaged relative to the reproducing dominant individuals. These benefits could either be direct, for example, “queuing” for a chance to occupy the dominant reproductive role; or indirect, for example, by boosting the fitness of dominant individuals to whom they are closely related (Cant and English 2006; Field and Cant 2009; Nonacs and Hager 2011). However, even when the benefits

Address correspondence to B.A. Taylor. E-mail: benjamin.taylor.16@ucl.ac.uk.

of helping are well-established, it remains the case that subordinate individuals typically gain significantly lower fitness returns than dominant individuals, resulting in potentially high conflict over access to dominant reproductive role(s). A complete understanding of the evolution of cooperative breeding therefore requires that we understand not just the benefits of helping, but also the mechanisms by which conflict between individuals is resolved.

The loss of a reproductive dominant opens up opportunities for conflict within otherwise stable societies. Subordinate individuals may compete for the newly vacant reproductive role, but this competition is likely to come at a cost to the group as a whole (Gobin et al. 2003; Strassmann et al. 2004). It is thus possible that selection will favor the evolution of mechanisms that facilitate the replacement of lost dominant individuals without outright conflict (Aureli and de Waal 2000; Aureli et al. 2002). Subordinate individuals may instead compete for a vacant reproductive role via “conventional” traits that serve to differentiate between candidates reproductives without direct conflict. For example, while dominance and reproductive succession are determined by aggressive interactions in many vertebrate societies (e.g., Creel et al. 1992; Clarke and Faulkes 1997; Nichols et al. 2012), in other societies wholly or partially conventional phenotypic traits such as song complexity, age, or length of tenure may serve as cues to dictate dominance without the need for outright conflict (e.g., East and Hofer 1991; Spencer et al. 2004; Duncan et al. 2018). Likewise, evidence exists for both conflict-based and convention-based reproductive succession mechanisms in invertebrate societies. Injurious fights over queen succession are particularly likely to occur when candidate reproductives are unrelated, as in the case of pleometrosis in ants (e.g., Bernasconi and Strassmann 1999) or multiple-foundress nesting in social wasps (e.g., West-Eberhard 1969). Reproductive succession in invertebrate groups with higher relatedness appears to more often involve traits such as age (e.g., Bridge and Field 2007). Evidence for the role of age in predicting dominance is particularly strong in *Polistes* paper wasps (Pardi 1948; Strassmann and Meyer 1983; Miyano 1986; Hughes and Strassmann 1988; Tsuji and Tsuji 2005) but it remains unclear whether the role of this trait in fact reflects differences in, for example, fighting ability or ovarian development, or whether it represents a genuinely arbitrary convention.

In-depth analysis of the social dynamics of reproductive replacement in cooperatively breeding societies requires the collection of detailed behavioral and physiological data that are not readily available for most vertebrates. By contrast, cooperatively breeding invertebrate societies such as those of *Polistes* paper wasps are relatively small, short-lived, and easily manipulable, making them excellent systems with which to analyze the dynamics of reproductive conflict resolution (Starks and Turillazzi 2006; Jandt et al. 2014).

While several studies have involved observations of *Polistes* colonies from which queens have either been experimentally removed or naturally lost, few of these have paid close attention to the social dynamics that give rise to replacement reproductives. In particular, only a very small number of studies have investigated the mechanisms of queen succession in nests following the eclosion of workers (Table 1). Reproductive conflicts during this worker phase may be radically different from those that occur during the founding phase because workers are usually closely related to one another and to the queen, which subordinate foundresses may not be (Zanette and Field 2008; Leadbeater et al. 2011).

The close relatedness among siblings within post-eclosion nests means that fitness interests of individuals in such groups are more

strongly aligned than in foundress groups, where relatedness can be low (Zanette and Field 2008; Leadbeater et al. 2011); this may have favored the evolution of more robust conflict–resolution mechanisms in post-eclosion nests. Unlike clonal social organisms (e.g., social aphids Uematsu et al. 2013), however, groups of *Polistes* workers are not genetically identical and so some degree of selfish behavior may persist. The intermediate level of relatedness observed among group members in post-eclosion paper wasp colonies thus contributes to their value as a model for the tradeoff between cooperation and conflict.

The European paper wasp *Polistes dominula* is the most intensely-studied species within its genus (Starks and Turillazzi 2006; Jandt et al. 2014), and partial evidence exists for both convention-based and contest-based resolution mechanisms following queen succession in this species (Table 1). We thus chose *P. dominula* as a focal system with which to perform an in-depth analysis of the queen replacement process in *Polistes*. We focused our analyses upon colonies following the emergence of the first adult workers, because we expected the higher within-colony relatedness during this phase to favor the expression of mechanisms that mitigate group-level costs during queen replacement.

In this paper, we conduct a detailed analysis of the social dynamics of queen succession in *P. dominula*. By removing queens from monogynous colonies, we generate detailed data on behavioral and ovarian development with which we test several hypotheses pertaining to the social mechanisms of queen replacement in this species. First, we determine the individual-level traits that dictate queen succession. We predict that queen succession is explained either by age, which is known to influence dominance in many *Polistes* (Pardi 1948; Strassmann and Meyer 1983; Miyano 1986; Hughes and Strassmann 1988; Tsuji and Tsuji 2005), suggesting convention; or alternatively by size, a trait thought to influence fighting ability in *Polistes* (Turillazzi and Pardi 1977; Cervo et al. 2008; Tibbetts and Shorter 2009; but see Reeve et al. 2000; Cant et al. 2006), suggesting contest (**Hypothesis 1**). Additionally, we test the hypothesis that queen succession reflects pre-existing physiological constraints on ovarian development (**Hypothesis 2**). Second, we examine group-level responses to queen removal to contextualize the succession process. We predict that queen removal will be followed by significant social disruption if succession is dictated by conflict but not if it is dictated by convention (**Hypothesis 3**). We investigate the distribution of behavioral responses to queen removal: these should be evenly distributed among multiple individuals within each colony under a contest-based succession mechanism, whereas in the case of convention-based succession only one or a few individuals should undergo significant behavioral changes (**Hypothesis 4**). We also test the hypothesis that group-level responses to queen removal will be minimized when there is reduced ambiguity regarding the identity of the replacement queen (**Hypothesis 5**). Hypotheses 1, 3, and 4 address whether the process of queen replacement is dictated by contest or convention (Table 2), while Hypotheses 2 and 5 investigate the proximate mechanisms of this succession process.

## METHODS

### Colony collection and aging of wasps

*Polistes dominula* colonies ( $N = 76$ ) were collected from rural areas near Florence, Italy, and transferred to a laboratory in the University of Florence during mid-May 2017, before the emergence of the first brood. Only nests with at least 20 cells and at

**Table 1**  
Review of published literature examining the effects of queen loss in postemergence *Polistes* colonies

Paper	Species	Data type: behavioral (B)/Genetic (G)/Ovarian (O)/Chemical (C)	Subordinate foundresses present?	Evidence for conflict		Evidence for convention	
				Fighting	Colony disruption	Conventional cues	Lack of colony disruption
Hughes et al. (1987)	<i>Polistes annularis</i>	B	Both considered	Y			Y
West-Eberhard 1969	<i>Polistes canadensis</i>	O	N		Y		
Miyano 1986	<i>Polistes chinensis</i>	B	N	Y	Y	Y	
Dapporto et al. 2005	<i>Polistes dominula</i> <sup>a</sup>	OC	N				
Strassman et al. 2004	<i>Polistes dominula</i> <sup>a</sup>	BO	N	(Y)	Y		
Monnin et al. 2009	<i>Polistes dominula</i> <sup>a</sup>	BO	Y				Y
Tibbetts and Huang 2010	<i>Polistes dominula</i> <sup>a</sup>	BC	N	(Y)			
Strassman and Meyer 1983	<i>Polistes exclamans</i>	B	N	(Y)		Y	
West-Eberhard 1969	<i>Polistes fuscatus</i>	O	N		Y		
Reeve and Gamboa 1983	<i>Polistes fuscatus</i>	B	N		(Y)		
Page et al. 1989	<i>Polistes fuscatus</i>	BO	Not reported				
Pardi 1948	<i>Polistes gallicus</i> <sup>b</sup>	BO	Both considered			Y	
Hughes and Strassman 1988	<i>Polistes instabilis</i>	BO	N			Y	
Miyano 1991	<i>Polistes jadwigae</i>	BO	N	Y	Y	Y	Y
Metcalf and Whitt 1977	<i>Polistes metricus</i>	G	Both considered				(Y)
Metcalf 1980	<i>Polistes metricus</i>	BG	N				
Hagiwara and Kojima 2002	<i>Polistes nipponensis</i>	B	N				
Metcalf 1980	<i>Polistes variatus</i>	BG	N				

*Fighting*: evidence of fighting between potential successors. *Colony disruption*: evidence of significant disruption to colony functioning or growth following queen loss. *Conventional cues*: evidence that traits other than size or fighting ability predict queen succession. *Lack of colony disruption*: evidence that colony functioning or growth are unaffected by queen loss. *Parentheses indicate partial evidence*. Fuller details are provided in the Supplementary Table S13.

<sup>a</sup>*P. dominula* is frequently referred to as *P. dominulus*.

<sup>b</sup>*P. gallicus* and *P. dominula* are difficult to distinguish and were not widely recognized as separate until ~1980; it is thus possible that Pardi's (1948) data actually derive from *P. dominula*.

**Table 2**  
Summary of predictions for Hypotheses 1, 3, and 4

	Convention	Conflict
<b>H1: Cues predicting queen succession</b>	Traits not directly related to competitive ability (e.g. age)	Correlates of fighting ability or resource holding potential (e.g. body size, aggression)
<b>H3: Extent of social disruption following queen removal</b>	Minimal	Substantial
<b>H4: Distribution of behavioral responses to queen removal</b>	Restricted to one or a few individuals	More evenly distributed among multiple competing individuals

least one capped cell were collected. *Polistes dominula* wasps typically do not initiate flight when the ambient temperature is below ~22 °C (Weiner et al. 2011) and colonies were therefore collected in the morning when temperatures were still low (<20 °C) to ensure that all nestmates were collected together. Colonies were maintained in glass boxes (15 cm × 15 cm × 15 cm) under natural light conditions with ad libitum access to water, sugar, dipteran larvae, and nest materials (cardboard and paper). On cool days (mid-day temperatures <25 °C), heaters were used to maintain high daytime temperatures within the laboratory; otherwise, temperatures were ambient. Immediately after colony collection, individuals were given unique markings by applying spots of colored paint (Testor Corporation) to the thorax and/or to the tips or upper portions of the wings.

Both single foundress (monogynous) and multi-foundress (polygynous) colonies were collected (mean 1.9 foundresses/colony; range 1–5 foundresses/colony). In order to ensure that all adult offspring emerged into an equivalent social environment on each colony, all subordinate foundresses were removed from the multiple-foundress

colonies. This loss of subordinate foundresses is not an unnatural state for *Polistes* colonies, which experience high rates of foundress loss in the wild (Strassmann 1981; Miyano 1986; Strassmann et al. 2004). Colonies were observed for 5 min hourly for 2 days following relocation to the lab in order to identify the dominant foundress. Dominant foundresses were identified based on two criteria: firstly, the dominant spends the large majority of her time on the nest and occupies the central portion of the nest carton, while her subordinate co-foundresses forage (Baracchi 2017); secondly, dominant individuals could be observed antennating subordinate individuals (see Methods; Pardi 1948; Jandt et al. 2014), while subordinates were never observed antennating dominants. In all cases, the dominant foundress of a colony was identified within 2 days of collection and before the eclosion of adult workers. Once the dominant foundress of a colony had been identified, all subordinates were removed from the nest box. Colonies were then checked daily and any newly emerged individuals were given unique identification markings. This allowed us to assign ages to each emerging individual in each colony, to an accuracy of 24 h.

## Queen removal experiments

Mature colonies were randomly allocated either to a queen removal (QR), or to a control (C) treatment. Control colonies were subjected to a sham removal in which an individual was removed from and then immediately placed back onto the nest. To capture the process of queen succession, we further randomly separated colonies into those in which we sampled wasps and assessed their reproductive dominance early during the succession period and those where this was done late in succession. A previous queen removal study in *P. dominula* (Strassmann et al. 2004) found that the process of queen replacement is ongoing at 3 days following queen loss but largely complete after 12 days. In line with this, we chose three and 12 days following queen removal as focal timepoints for our analyses. The four treatments are henceforth referred to as QR3 ( $n = 20$ ), QR12 ( $n = 20$ ), C3 ( $n = 20$ ), and C12 ( $n = 15$ ).

A colony was considered “mature” once it had produced a minimum of four adult offspring (Dapporto et al. 2005). Each colony was manipulated according to its treatment group on the morning of the fourth day following maturity. All manipulations were performed between 07:00 and 08:00, during which time period the temperatures in the lab were still well below 22 °C. For colonies belonging to QR3 or QR12 treatments, manipulation consisted of removing the queen and immediately preserving her body in a 1.5 mL Eppendorf tube containing 80% EtOH, which was stored at –20 °C for later dissection. For C3 and C12 treatments, manipulation consisted of removal of a randomly preselected nonfoundress individual. Following this manipulation, each colony was maintained under standard lab conditions for an additional period of time dictated by treatment group: 3 days for QR3 and C3 colonies, and 12 days for QR12 and C12 colonies.

## Data collection

### Ovarian and body size measurements

All individuals were dissected after completion of the experiment. For each individual, an index of ovarian development was obtained by removing and photographing the ovarioles, and subsequently measuring the mean length of the six largest oocytes/ova present. This is a standard measure of ovarian development and has been shown to strongly correlate with more complex ovarian indices in *P. dominula* (Cini et al. 2013). Individuals with extremely underdeveloped oocytes (all oocytes <15 µm in length) were assigned an ovarian index of 15 µm as measurements were imprecise below this value.

We obtained measures of body size by removing the left forewing of each individual and measuring the maximum distance from the tip of the wing to the thoracic wing joint, which is a reliable proxy for body size in *Polistes* wasps (Haggard and Gamboa 1980; Cant et al. 2006). Wing length was used in place of head width because head tissues had been consumed in a separate analysis. All measurements were performed using *Fiji*, a distribution package of the image processing program *ImageJ* 1.52 (Schindelin et al. 2012; Schneider et al. 2012). All measurements were performed by a single observer, blind with respect to each individual’s identity and treatment group.

### Behavioral recording of nestmate interactions

To obtain data regarding the individual- and group-level mechanisms of queen replacement, we recorded the individuals’ behavior before and after manipulation. Colonies were filmed before and after experimental manipulation in order to assess individual-level and group-level effects of queen loss. Recordings were made for

30 min daily for 3 days before and 3 days after experimental manipulation, using Sony HDR-CX405 HD video cameras mounted on tripods. Additionally, colonies in the QR12 and C12 treatments were filmed for 30 min daily on days 10 through 12 following experimental manipulation. All filming occurred between the hours of 10:30 and 16:30 when *P. dominula* activity levels are at their highest (Cini et al. 2013). The time of filming for each colony and day was randomized. Between 07:00 and 08:00 on the morning following the end of the treatment-specific time period, the entire colony was terminated by removing all individuals and preserving their bodies in alcohol as described above.

Digitally recorded behaviors for each colony were annotated using BORIS observation software (Friard and Gamba 2016). To permit efficient analysis of the >200 h of videos recorded, behaviors not directly related to dominance interactions (e.g., nest building) were not recorded. An observer recorded the time and duration of each instance of dominance behavior that occurred within each video, and also tracked the proportion of time spent on and off the nest carton by each individual within each 30-min video. In line with previous behavioral observations of *P. dominula* colonies, mounting followed by antennation was by far the most common behavior observed at all treatment stages (Pardi 1948; Tibbetts and Huang 2010; Jandt et al. 2014). More aggressive dominance interactions, such as wing chewing, were observed extremely rarely (<20 times across the entire experiment) and so, all subsequent analyses focus solely on mounting followed by antennation (hereafter referred to simply as “antennation”).

To reduce the likelihood of false positives, antennation bouts were only recorded if they were longer than 1 s in duration. Antennation bouts that did not occur in conjunction with an unambiguous instance of mounting were not recorded, as these may simply reflect affiliative or communicative functions rather than dominance behavior. In each instance of antennation, the dominant and subordinate individuals’ identities were recorded. Dominant and subordinate actors in a bout of antennation are usually easily identified: the dominant strikes the subordinate with her antennae while the subordinate remains still and lowers her head and body to the nest surface (Pardi 1948; Jandt et al. 2014). In a small proportion (~5%) of antennation bouts, antennation was resisted by the targeted individual, resulting in an inconclusive struggle between the two individuals without either establishing a clear dominant role. For the purposes of downstream social network analyses, these bouts were recorded as draws.

In order to test whether queen removal results in a group-level change in dominance behavior, we calculated the mean and variance of antennation rate within each colony for each 3-day time period. We additionally calculated the average proportion of time individuals spent off the nest carton (a proxy measure of participation in off-nest activities such as foraging or internidal drifting) for each time period, to test whether queen removal exacts a cost in terms of the group’s ability to continue normal colony functions. As interactions were only recorded when they occurred on the nest carton itself, antennation rate was measured relative to the amount of time that an individual was present on the nest.

## Analyzing the process of queen succession

### Assignment of Elo ratings to estimate within-group dominance

We used the Elo rating system (Elo 1978; Albers and De Vries 2001; Neumann et al. 2011) to determine a dominance score for

each individual within each observation period. The Elo rating system assigns each individual an equal, arbitrary starting value and then uses the results of sequential pairwise interactions, each with a winner and loser, to adjust the individuals' values based on the discrepancy between the actual outcome of the interaction and that expected from previous interactions. Thus, an individual experiences a large gain in Elo rating if she wins unexpectedly (i.e., if she defeats an individual of higher prior Elo value than herself), but only a small gain if she was already expected to win the contest (i.e., if she already has a higher Elo value than the individual she defeats). Elo ratings are well-suited to our data, as they can accommodate repeated interactions between specific pairs of individuals.

We collated all observed behaviors for a given colony within each of three set time periods: the 3 days prior to manipulation, the 3 days immediately following manipulation (for all colonies), and days 10 through 12 following manipulation (for QR12 and C12 colonies only). We then generated Elo rankings for each individual during each period using the *AniDom* package in R (Farine and Sanchez-Tojar 2018) with an initial Elo value of 1000 and scaling constant  $K = 100$ . Elo rankings are sensitive to the order of interaction, but each video represents only a small portion of the total number of interactions that may have occurred within a 3-day period and the order of in which interactions were observed may not have been meaningful. To remove potential bias, we therefore randomly re-ordered the list of contests collated within each 3-day period 1000 times and obtained an Elo ranking for each individual for each permutation; final Elo scores were then calculated as the mean score across all permutations for the given time period. Each time period (3 days pre-removal, and days 1–3 and 10–12 post-removal) was treated as independent. In addition, we discarded dominance values for any individual that was observed on the nest carton for fewer than 30 min within the focal 3-day time period rather than arbitrarily assign “neutral” Elo scores to individuals that were under-observed.

### Social network analyses

As a complement to individual-level measures of dominance, we used social network analyses to capture group-level consequences of queen removal. Network characteristics were calculated using the behavioral interactions for each colony for each 3-day period, again treating each period as independent. Collated lists of behavioral interactions were converted to social networks in R using the *igraph* package (Csardi and Nepusz 2006) with each individual representing a node and each interaction representing an edge (connection) between nodes. For each network, we then generated two measures of social network structure. The *transitivity coefficient* (or *clustering coefficient*) of a network measures the global density of closed node triads, that is, the proportion of instances in which, when an individual A has interacted with two other individuals B and C, those two individuals have also interacted with one another. Transitivity may be interpreted as a measure of the cohesiveness of the group (Croft et al. 2008). *Degree centrality* is the extent to which a particular node (individual) occupies a central location within a network (Croft et al. 2008). Variance in degree centrality indicates the level of social monopoly within a group, and high-degree centrality variance indicates that one or a few individuals dominate the network relative to a larger number of poorly connected individuals. If new queens establish themselves by directing frequent dominance behavior toward their nestmates, then we should expect to observe an increase in the variance of degree centrality in colonies following queen removal.

### Estimation of individual-level transition from worker to queen roles

In order to robustly assign queen identity, we fit a Bayesian logistic regression model with the R package *arm* (Gelman and Su 2018) using ovarian development indices and Elo ratings from queens and workers from queenright control colonies as the independent variables and caste as a binary response variable. This allowed us to subsequently estimate the degree to which individuals on postremoval colonies phenotypically resembled workers or queens. Workers were coded with a value of 0 and queens were coded with a value of 1. We applied a flat Bayesian prior to the model output to account for the fact that phenotypic scores for workers and queens exhibit perfect separation on queenright colonies (Gelman et al. 2008), whereas our expectation is that workers transitioning to queens must necessarily pass through some intermediate stage in which their phenotype is wholly or partially intermediate between that of a “normal” queen and “normal” worker. For each QR3 and QR12 colony, we then estimated the “queenness” of each individual by supplying the model with ovarian scores and dominance scores pertaining to the 3 days prior to colony termination. Using this method, each individual from each QR3 and QR12 colony was assigned a value from 0 to 1 indicating the degree of phenotypic identity to workers or queens from queenright colonies (0 = 100% similarity to worker phenotype; 1 = 100% similarity to queen phenotype), except where Elo ratings could not be established due to insufficient observational data.

### Testing the hypotheses

General linear mixed models (GLMMs) except those with queenness as the response were constructed in R using the *lmer* function, part of the package *lme4* (Bates et al. 2015). For individual-level analyses, response variables were queenness (Section 2.4.3), Elo rating, or ovarian development. Models with queenness as the response were constructed using the *metafor* R package (Viechtbauer 2010), which allowed us to weight individuals' queenness estimates by the inverse of the standard error of those estimates. For all individual-level models, fixed effects were wing length, age and premanipulation Elo rating and their pairwise interactions. The possibility that caste-biased traits such as ovarian development might be negatively correlated within nests (if, e.g., replacement queens suppress their nestmates' phenotypic plasticity) led us to question the validity of including colony as a random effect in the individual-level models. To account for this, we ran each individual-level model both with and without the random effect. We report the results of the latter fixed-effect models alongside the mixed-effect models in the [Supplementary Materials](#).

For group-level analyses, response variables were within-group mean antennation rate, antennation rate variance, network transitivity, degree centrality, or mean time off-nest. Fixed effects were treatment group (Control vs. Queen removal), and experimental stage (premanipulation vs. postmanipulation days 1–3 vs. postmanipulation days 10–12), number of individuals in the colony, and the interaction between treatment and time period. Colony was included as a random factor in each model, to account for repeated measurements of the same colonies, which were assumed to be independent. For group-level analyses, response variables were transformed using Tukey's ladder of powers transformation ( $\lambda = 0.450, 0.175, 0.925, 0.950, \text{ and } 0.775$ , respectively for mean, variance, transitivity, centrality, and time off-nest transformations),

and were thereafter confirmed to adhere adequately to the assumption of normality using the package *rcompanion* (Mangiafico 2018). In all cases, continuous variables were centered and scaled to facilitate model comparison. Full details and results for each model are given in the [Supplementary Tables S3–S12](#).

## RESULTS

Of 76 colonies collected, eight were excluded due to colony failure: six did not produce the minimum required number of four adult workers within 21 days of collection, and in a further three the queen died before the emergence of the first brood. Additionally, we excluded 12 colonies that were heavily styliposed by strepsipteran flies (*Xenos vesparum*), defined as displaying >50% styliposition among all offspring produced across the course of the experiment. Following these exclusions, final colony sample sizes for the experiment were  $n = 55$  colonies, with  $n = 16$  colonies each for treatments QR3, QR12, and QC3, and  $n = 7$  colonies for treatment QC12.

Approximately half of the remaining 55 colonies produced at least one styliposed individual (mean  $\pm$  SE  $1.56 \pm 0.28$  styliposed wasps/colony across all 55 colonies, representing  $13.6 \pm 2.1\%$  of workers in each colony). Styliposed individuals become asocial, fail to perform typical foraging and feeding behaviors, and eventually disperse from the nest (Hughes et al. 2004; Dapporto et al. 2007; Kathirithamby 2009; Beani et al. 2011; Geffre et al. 2017). Styliposed individuals do not typically engage in or respond to dominance interactions, and disperse within a few days of emergence (Hughes et al. 2004). Here, they comprised 12% (86/701) of experimental individuals but took part in a total of just 0.3% (56/1633) observed dominance interactions. Accordingly, we excluded styliposed individuals from further analysis.

A very small number of males emerged during the experiment (3/701 observed individuals). Since male *P. dominula* very rarely engage in dominance behavior (5/1633 observed dominance interactions in this experiment) and are known to disperse relatively quickly following eclosion in nature (Reeve 1991), we excluded males from all analyses.

Following these exclusions, behavioral and ovarian data for 55 queens and 557 workers from 55 colonies remained (mean  $\pm$  SE  $12.2 \pm 0.66$  wasps/colony; [Supplementary Tables S1 and S2](#)).

### Hypothesis 1: predictors of queen succession

Age was the sole significant predictive variable in each of the three complete models of individual phenotypes following queen removal, suggesting that age is a reliable predictor of both postremoval ovarian development (Est = 0.43, SE = 0.12,  $P = 0.0023$ ) and postremoval dominance (Est = 0.28, SE = 0.10,  $P = 0.008$ ), and thus of postremoval queenness (Est = 0.17, SE = 0.044,  $P < 0.001$ ; [Supplementary Table S3](#)). The slope of queenness on age was similar when models were constructed using data from QR3 colonies only (Est = 0.18, SE = 0.15,  $P = 0.22$ ) or from QR12 colonies only (Est = 0.14, SE = 0.11,  $P = 0.21$ ; [Supplementary Table S4](#)).

Excluding two colonies which failed to produce any candidate queen replacements (see **Hypothesis 3** below), in 19/30 (63%) queen removal colonies the individual with the highest queenness was also the oldest individual ([Figure 1](#)). In a further 8/30 (27%) colonies, this individual was the second oldest, leaving three colonies in which neither of the two oldest individuals was the most queenlike. These proportions did not differ between QR3 and QR12 treatments ( $\chi = 0.89$ ,  $P = 0.64$ ; [Supplementary Table S5](#)). Thus, while

age appears to act a strong predictor of succession, it does not perfectly explain variation between individuals' caste identities.

Neither body size (measured by wing length) nor premanipulation Elo rating emerged as significant terms in any of the models, indicating that queen succession in *P. dominula* is unlikely to be strongly dictated by physical strength. A possible exception appeared in the model with postmanipulation Elo rating as the response variable, in which there was a near-significant negative interaction between body size and age (Est. =  $-0.18$ , SE = 0.10,  $P = 0.074$ ; [Supplementary Table S3](#)). This might plausibly indicate that for particularly large individuals, age is a less important determinant of dominance following queen removal.

### Hypothesis 2: role of ovarian development in queen succession

Contrary to the hypothesis that post-eclosion queen succession in *Polistes* reflects inherent physiological constraints upon ovarian development in workers, when we included control colonies in our ovarian model, we found no evidence for a relationship between age and ovarian development on queenright colonies (Est. = 0.060, SE = 0.096,  $P = 0.53$ ; [Figure 2](#); [Supplementary Table S6](#)). Only following queen loss did older individuals begin to display greater ovarian development than their younger sisters (Est. = 0.52, SE = 0.12,  $P < 0.001$ ).

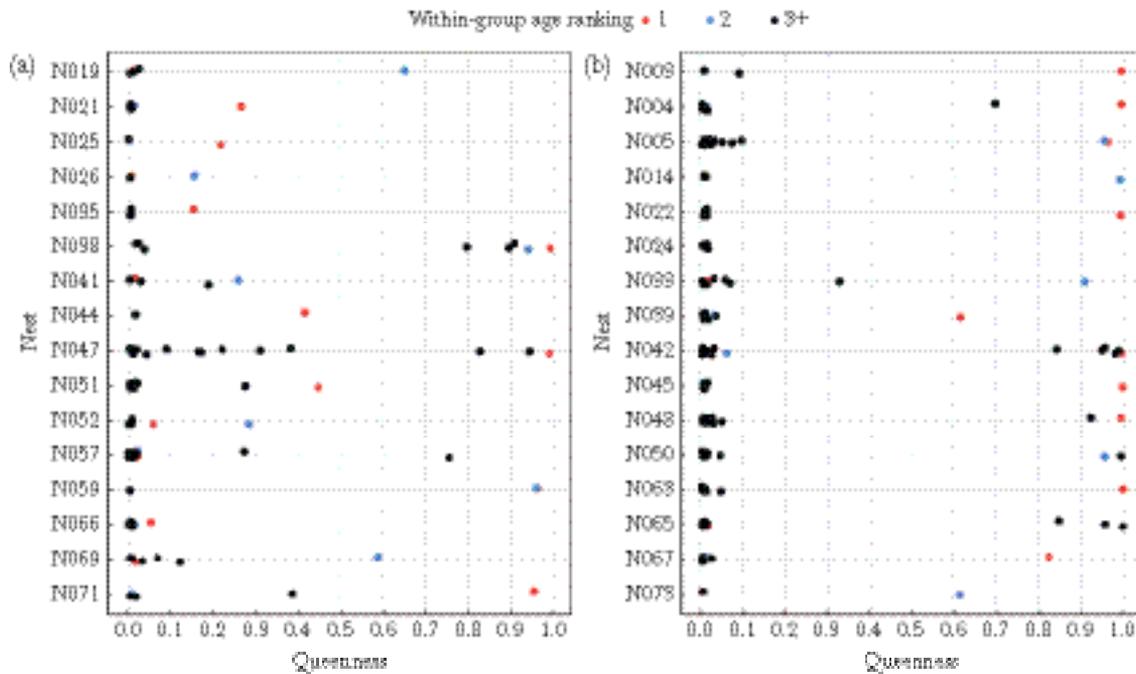
### Hypothesis 3: group-level resilience to queen loss

We found little evidence that queen removal significantly altered the group-level social dynamics within colonies. Neither mean (Est. = 0.24, SE = 0.27,  $P = 0.37$ ) nor variance (Est. = 0.12, SE = 0.11,  $P = 0.28$ ) of antennation rates were significantly increased following queen removal, indicating that loss of the dominant does not result in a meaningful increase in the rate and variance of dominance behavior ([Supplementary Table S7](#), [Figure 3](#)).

Both social network centrality (Est. = 0.49, SE = 0.28,  $P = 0.089$ ) and clustering coefficient (Est. = 0.63, SE = 0.37,  $P = 0.091$ ) exhibited borderline-significant increases in the 3 days following queen removal, but we otherwise found no evidence of group-level responses to queen loss ([Supplementary Table S8](#)). By contrast, control colonies exhibited significantly decreased centrality (Est. =  $-0.76$ , SE = 0.33,  $P = 0.022$ ) and increased mean time off-nest (Est. = 1.1, SE = 0.41,  $P = 0.0096$ ) at days 10–12 following manipulation ([Supplementary Table S8](#)).

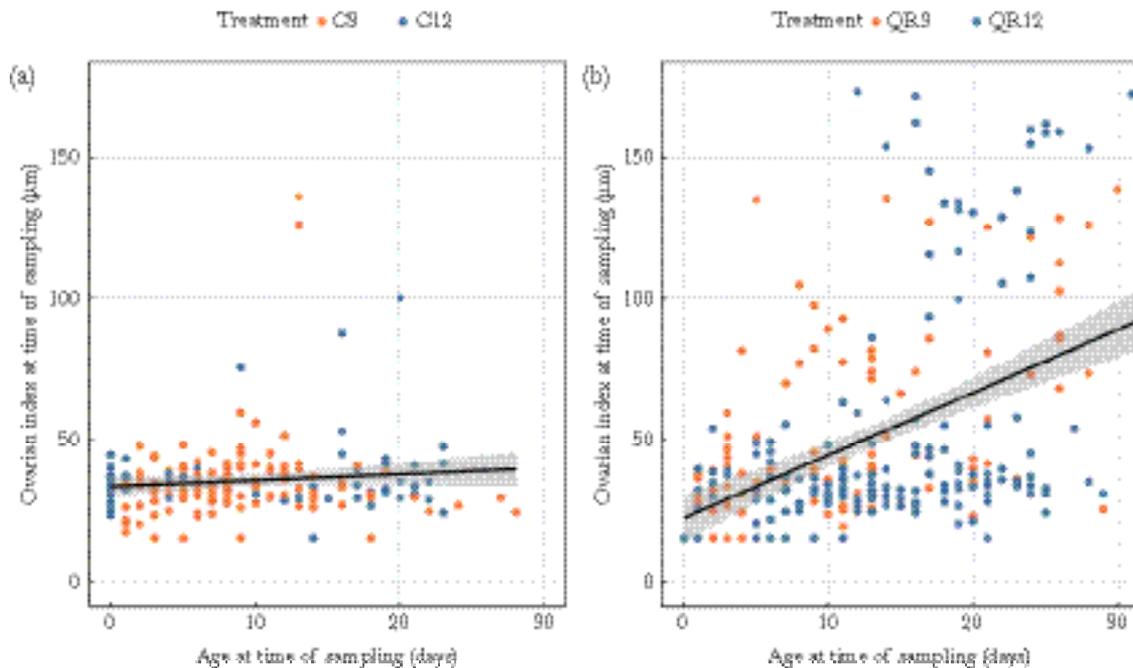
Network centrality (Est. = 0.20, SE = 0.028,  $P = <0.001$ ) and mean (Est. = 0.16, SE = 0.034,  $P = <0.001$ ) and variance (Est. = 0.065, SE = 0.014,  $P < 0.001$ ) of antennation rate were all strongly positively correlated with colony size.

One notable manner in which queen loss may have altered nests' social structures was in the production of multiple replacement queens. A large majority of individuals on postremoval colonies were assigned queenness values very close to zero, as expected if most individuals remain as un-reproductive, low-dominance workers. We thus considered any individual with a queenness estimate greater than 0.1 to be exhibiting significantly divergent caste expression relative to the normal worker profile; any such individual might represent a potential replacement queen. While the majority of nests produced either one (15/32 nests) or two (11/32) potential replacement queens, a small number (4/32) produced three or more replacements, and a further 2/32 failed entirely to produce a potential replacement queen. These numbers did not differ significantly between QR3 and QR12 conditions ( $\chi = 0.16$ ,  $P = 0.98$ ; [Supplementary Table S9](#)).



**Figure 1**

Queenness estimates for individuals from (a) QR3 and (b) QR12 nests. Colored points represent the oldest (red) and second-oldest (blue) individuals from each nest.



**Figure 2**

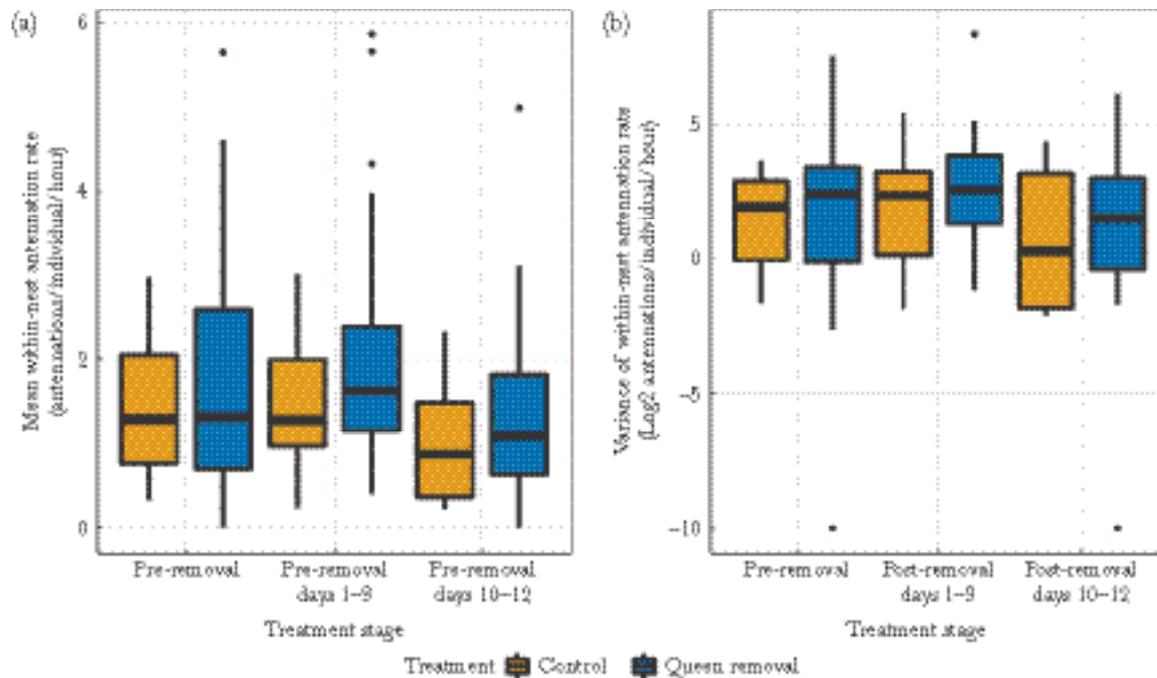
Ovarian index plotted against age for workers from (a) control and (b) queen removal colonies. Trend lines with 95% confidence intervals are shown in black.

#### Hypothesis 4: within-group distribution of behavioral responses to queen removal

In accordance with the predictions of a convention-based succession model, the change in individuals' antennation rates between the 3 days preceding and the 3 days following queen removal was strongly predicted by age (Est. = 1.2, SE = 0.22,  $P < 0.001$ ), although there was also a strongly significant negative interaction

between the effects of body size and age (Est. =  $-0.69$ , SE = 0.22,  $P = 0.0018$ ; Supplementary Table S10). This negative interaction term indicates that age was a weaker predictor of antennation rate for larger individuals.

The mean increase in dominance rates was close to zero for the youngest (latest-eclosing) individuals on each colony: an increase of 0.09 antennations/hour for individuals that were fifth or below in the order of eclosion versus an increase of 2.42 antennations/hour



**Figure 3**

(a) Mean and (b) log<sub>2</sub> variance of within-colony antenation rates. Neither mean nor variance of within-colony antenation rate vary significantly with stage or treatment.

for individuals that eclosed first or second on their respective colonies, and an increase of 0.71 for those that eclosed third or fourth.

### Hypothesis 5: efficacy of gerontocracy in the presence of low age rank resolution

Age-based convention appears to act as an effective means of conflict mitigation during queen succession in *P. dominula*. Despite this, we found no evidence that a lack of resolution within a colony's age hierarchy results in the failure of this conflict-resolution mechanism, that is, a reversion to a contest-based system. The age gap between the two oldest workers in a colony was not a significant predictor of the increase in antenation rate in that colony in the 3 days immediately following queen removal (Est. = 0.50, SE = 0.40,  $P = 0.22$ ; Supplementary Table S11), suggesting that colonies with multiple oldest individuals of similar ages are nonetheless able to transition to a successor queen without a significant increase in intragroup conflict. We also found no correlation between the difference in antenation rates of the two most dominant workers on a colony prior to queen removal and increases in colony-wide antenation rate on that same colony following queen removal (Est. = -0.22, SE = 0.43,  $P = 0.62$ ; Supplementary Table S12).

## DISCUSSION

The potential future benefit of inheriting the reproductive role is thought to be an important factor ensuring the ongoing cooperation of helpers in societies with high reproductive skew. Despite this, the mechanisms by which replacement reproductives arise in cooperative societies are not well understood. Here, we have presented the results of the most in-depth analysis of the mechanisms of reproductive succession in an invertebrate society to date. In addition to confirming that queen succession among workers in *P. dominula*

is dictated by age, we show that this gerontocratic system is not underlain by age-dependent constraints upon size or reproductive development. We additionally provide evidence that group-level characteristics, such as the rate and network structure of dominance interactions between individuals, are not strongly perturbed by queen loss. Behavioral responses to queen removal were concentrated among the oldest individuals, suggesting that the gerontocratic convention effectively mitigates potentially costly conflict over reproductive succession in post-eclosion colonies of this species.

Age acted as a strong predictor for queen succession, both strongly predicting individuals' chances of inheriting the queen position and seemingly moderating social disruption following queen loss. Despite this, we did not find evidence that groups were less able to mitigate within-colony conflict when the strength of this cue was relatively weak. Groups with a poorly resolved age ranking did not experience greater social disruption than ones in which the age gap between the oldest individuals was large. Moreover, the most queenlike individual on a given nest was not always the oldest, although in 90% of nests she was one of the two oldest individuals. Colonies were only maintained for a relatively short period of time in order to minimize any behavioral effects of the laboratory environment (Jandt et al. 2015), but as a result the age difference between individuals on any given colony was small. The influence of the gerontocratic convention identified here might be stronger on colonies that have undergone a larger number of brood cycles, with a larger range of ages therefore represented.

The very low level of group-level perturbation we observed following queen removal contrasts with results from Strassmann et al. (2004), who found significant increases in within-group conflict immediately following queen loss in mature nests outside the laboratory context. We consider three possible explanations for the discrepancy between these results and our own. First, colony size is known to predict conflict between dominant and subordinate individuals in *Polistes* (Cant et al. 2006), and thus, it may be that the early-stage nests we

observed were too small to merit conflict over succession. Second, it is possible that some aspect of the lab context, such as ad libitum access to food, reduced the propensity of individuals to engage in conflict. Finally, the fact that we enforced a single-foundress context upon our colonies in question may have been a factor. From the perspective of an early-emerging worker, the absence of subordinate foundresses on the nest may act as an indicator of particularly high within-nest relatedness, since in a monogynous colony the workers are guaranteed to be fully matrilineally related.

Intriguingly, we identified a strongly negative interaction between age and size in predicting the change in individuals' antennation rate following queen removal. Age was a weaker predictor of antennation rate increase for larger individuals, which might indicate that larger individuals were attempting to compete for the dominant position even while young. Despite this, there was no meaningful influence of size upon ovarian development or Elo rating. This suggests that the gerontocratic convention operates effectively even in the face of physically large competitors, at least for the early-season colonies described here. One possibility is that such "queue jumpers" might become more aggressive in their efforts later in the season when the indirect fitness benefits of cooperation have declined, as occurs in certain other reproductively plastic social insects such as bumble bees (Rottler-Hoermann et al. 2016).

Our results are consistent with the established notion that social hierarchies on queenright *P. dominula* colonies are age-based, with the oldest individuals being the most dominant (Pardi 1948; Theraulaz et al. 1990). The physiological bases of this age-based system have remained elusive, however. One established hypothesis is that gerontocracy in *P. dominula* reflects a physiological constraint, that is, that younger individuals might have underdeveloped ovaries and so as a result are poorly positioned to transition to a reproductive role (Pardi 1948). Contrary to this, our data show that the positive relationship between workers' age and ovarian development is present only following queen removal. This is what we would expect to observe if gerontocracy is antecedent to, rather than a consequence of, variation in ovarian development. Moreover, while *P. dominula* expresses a positive relationship between age and reproductive dominance, this is not the case in all *Polistes* species: several species are thought to express the reverse relationship, with younger individuals more likely to inherit the queen role, possibly due to ecological variables that affect future fitness payoffs (Tsuji and Tsuji 2005). The existence of age-based conventions acting in opposite directions in different *Polistes* species seems incongruent with the idea that ovarian development is limited by age in this genus, but is unsurprising if age acts as a predominantly arbitrary signifier of dominance.

The speed with which colonies appear to have generated replacement queens and the low-conflict nature of this transition indicate a remarkably robust and efficient conflict resolution mechanism operating within *P. dominula* colonies. Such robust mechanisms for the mitigation and resolution of intragroup conflict are essential components in the long-term maintenance of animal social groups (Aureli and de Waal 2000). Despite this, the nature of these mechanisms has been difficult to elucidate, especially outside of the nonhuman primates (Aureli et al. 2002). It has proven particularly challenging to separate different aspects of the phenotype in order to identify the specific cues that matter for reproductive succession in complex vertebrate societies within which measuring behavior and physiology is difficult and time consuming. Our ability to generate detailed phenotypic data for a large number of individuals over a short period of time was key in revealing the capacity for gerontocracy to act as a robust conflict-resolution system in a society with very high

reproductive skew. Though labor-intensive to produce even in an invertebrate system, such in-depth data will be necessary to advance our understanding of social conflict resolution.

Understanding how social cohesion is maintained in the face of within-group conflicts is a key project of social evolutionary biology, and social insects are among our best models for testing hypotheses in this field. The results presented here represent the most in-depth analysis of reproductive succession in a cooperatively breeding social insect to date. Our results confirm that the process of queen succession can occur with minimal social disruption, and we provide strong evidence in favor of the hypothesis that reproductive succession can be successfully dictated by a convention rather than by violent and costly within-group conflict. Our findings provide novel insights into the mechanisms by which social groups can mitigate potential sources of internal conflict.

## FUNDING

This work was supported by the Natural Environment Research Council (grant code NE/L002485/1).

The authors would like to thank F. Cappa, I. Pepicciello, L. Dapporto, and others at the Dipartimento di Biologia, Università di Firenze for assistance with field work, and members of the Sumner laboratory for comments on the manuscript. We additionally wish to thank Dr. L. Holman and an anonymous reviewer for their constructive comments.

Conflict of interest: The authors of this study declare that he has no conflict of interest.

Data accessibility: Analyses reported in this article can be reproduced using the data provided by Taylor et al. (2020).

**Handling editor:** Luke Holman

## REFERENCES

- Albers PCH, De Vries H. 2001. Elo-rating as a tool in the sequential estimation of dominance strengths. *Anim Behav.* 61(2):489–495.
- Aureli F, Cords M, Van Schaik CP. 2002. Conflict resolution following aggression in gregarious animals: a predictive framework. *Anim Behav.* 64(3):325–343.
- Aureli F, de Waal FBM. 2000. Why natural conflict resolution? In: Aureli F, de Waal FBM, editors. *Natural conflict resolution*. Berkeley (CA): University of California Press. p. 3–10.
- Baracchi D. 2017. The reproductive division of labour but not worker age affects spatial sorting within the nest in a paper wasp. *Insectes Soc.* 64(3):379–385.
- Bates D, Maechler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using lme4. *J Stat Softw.* 67(1):1–48.
- Beani L, Dallai R, Mercati D, Cappa F, Giusti F, Manfredini F. 2011. When a parasite breaks all the rules of a colony: morphology and fate of wasps infected by a strepsipteran endoparasite. *Anim Behav.* 82(6):1305–1312.
- Beekman M, Komdeur J, Ratnieks FLW. 2003. Reproductive conflicts in social animals: who has power? *Trends Ecol Evol.* 18(6):277–282.
- Bernasconi G, Strassmann JE. 1999. Cooperation among unrelated individuals: the ant foundress case. *Trends Ecol Evol.* 14:477–482.
- Bridge C, Field J. 2007. Queuing for dominance: gerontocracy and queue-jumping in the hover wasp *Liostenogaster flavolineata*. *Behav Ecol Sociobiol.* 61(8):1253–1259.
- Cant MA, English S. 2006. Stable group size in cooperative breeders: the role of inheritance and reproductive skew. *Behav Ecol.* 17(4):560–568.
- Cant MA, English S, Reeve HK, Field J. 2006. Escalated conflict in a social hierarchy. *Proc Biol Sci.* 273:2977–2984.
- Cant MA, Young AJ. 2013. Resolving social conflict among females without overt aggression. *Philos Trans R Soc Lond B Biol Sci.* 368:20130076.
- Cervo R, Dapporto L, Beani L, Strassmann JE, Turillazzi S. 2008. On status badges and quality signals in the paper wasp *Polistes dominulus*: body size, facial colour patterns and hierarchical rank. *Proc Biol Sci.* 275:1189–1196.

- Cini A, Meconcelli S, Cervo R. 2013. Ovarian indexes as indicators of reproductive investment and egg-laying activity in social insects: a comparison among methods. *Insectes Soc.* 60(3):393–402.
- Clarke FM, Faulkes CG. 1997. Dominance and queen succession in captive colonies of the eusocial naked mole-rat, *Heterocephalus glaber*. *Proc Biol Sci.* 264:993–1000.
- Creel S, Creel N, Wildt DE, Monfort SL. 1992. Behavioural and endocrine mechanisms of reproductive suppression in Serengeti dwarf mongooses. *Anim Behav.* 43(2):231–245.
- Croft DP, James R, Krause J. 2008. Exploring animal social networks. Princeton (NJ): Princeton University Press.
- Csardi G, Nepusz T. 2006. The igraph software package for complex network research. *InterJournal Complex Systems* 1695.
- Dapporto L, Cini A, Palagi E, Morelli M, Simonti A, Turillazzi S. 2007. Behaviour and chemical signature of pre-hibernating females of *Polistes dominulus* infected by the strepsipteran *Xenos vesparum*. *Parasitology.* 134:545–552.
- Dapporto L, Matthew Sledge F, Turillazzi S. 2005. Dynamics of cuticular chemical profiles of *Polistes dominulus* workers in orphaned nests (Hymenoptera, Vespidae). *J Insect Physiol.* 51:969–973.
- Duncan C, Gaynor D, Clutton-Brock T. 2018. The importance of being beta: female succession in a cooperative breeder. *Anim Behav.* 146:113–122.
- East ML, Hofer H. 1991. Loud calling in a female-dominated mammalian society: II. behavioural contexts and functions of whooping of spotted hyaenas, *Crocuta crocuta*. *Anim Behav.* 42(4):651–669.
- Elo AE. 1978. The rating of chess players, past & present. New York (NY): Arco.
- Farine DR, Sanchez-Tojar A. 2018. aniDom: Inferring Dominance Hierarchies and Estimating Uncertainty. R package version 0.1.3. Available from: <https://CRAN.R-project.org/package=aniDom>.
- Field J, Cant MA. 2009. Reproductive skew in primitively eusocial wasps: how useful are current models? In: Hager R, Jones CB, editors. Reproductive skew in vertebrates: proximate and ultimate causes. Cambridge: Cambridge University Press. p. 305–334.
- Friard O, Gamba M. 2016. BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. In: Fitzjohn R, editor. *Methods Ecol Evol.* 7(11):1325–1330.
- Geffre AC, Liu R, Manfredini F, Beani L, Kathirithamby J, Grozinger CM, Toth AL. 2017. Transcriptomics of an extended phenotype: parasite manipulation of wasp social behaviour shifts expression of caste-related genes. *Proc R Soc B Biol Sci.* 284(1852):20170029.
- Gelman A, Su YS. 2018. arm: data analysis using regression and multilevel/hierarchical models. R package version 1.10–2/r276.
- Gelman A, Jakulin A, Pittau MG, Su YS. 2008. A weakly informative default prior distribution for logistic and other regression models. *Ann Appl Stat.* 2(4):1360–1383.
- Gobin B, Heinze J, Strätz M, Roces F. 2003. The energetic cost of reproductive conflicts in the ant *Pachycondyla obscuricornis*. *J Insect Physiol.* 49:747–752.
- Haggard CM, Gamboa GJ. 1980. Seasonal variation in body size and reproductive condition of a paper wasp, *Polistes metricus* (Hymenoptera: Vespidae). *Can Entomol.* 112(3):239–248.
- Hagiwara Y, Kojima J. 2002. Reproductive options for first brood “workers” emerging in orphan nests of *Polistes nipponensis* (Hymenoptera, Vespidae). *Insectes Soc.* 49(3):191–5.
- Hughes CR, Beck MO, Strassmann JE. 1987. Queen succession in the social wasp, *Polistes annularis*. *Ethology.* 76(2):124–132.
- Hughes DP, Kathirithamby J, Turillazzi S, Beani L. 2004. Social wasps desert the colony and aggregate outside if parasitized: parasite manipulation? *Behav Ecol.* 15(6):1037–1043.
- Hughes CR, Strassmann JE. 1988. Age is more important than size in determining dominance among workers in the primitively eusocial wasp, *Polistes instabilis*. *Behaviour.* 107(1):1–4.
- Jandt JM, Thomson JL, Geffre AC, Toth AL. 2015. Lab rearing environment perturbs social traits: a case study with *Polistes* wasps. *Behav Ecol.* 26(5):1274–1284.
- Jandt JM, Tibbetts EA, Toth AL. 2014. *Polistes* paper wasps: a model genus for the study of social dominance hierarchies. *Insectes Soc.* 61(1):11–27.
- Kathirithamby J. 2009. Host-parasitoid associations in Strepsiptera. *Annu Rev Entomol.* 54:227–249.
- Krause J, Ruxton GD. 2002. Living in groups. Oxford (UK): Oxford University Press.
- Leadbeater E, Carruthers JM, Green JP, Rosser NS, Field J. 2011. Nest inheritance is the missing source of direct fitness in a primitively eusocial insect. *Science.* 333:874–876.
- Mangiafico S. 2018. rcompanion: functions to support extension education program evaluation. R package version 2.0.0. Available from: <https://CRAN.R-project.org/package=rcompanion>.
- Metcalf RA. 1980. Sex ratios, parent-offspring conflict, and local competition for mates in the social wasps *Polistes metricus* and *Polistes variatus*. *Am Nat.* 116(5):642–54.
- Metcalf RA, Whitt GS. 1977. Intra-nest relatedness in the social wasp *Polistes metricus*. *Behav Ecol Sociobiol.* 2(4):339–51.
- Miyano S. 1986. Colony development, worker behavior and male production in orphan colonies of a Japanese paper wasp, *Polistes chinensis antennalis* Pérez (Hymenoptera: Vespidae). *Res Popul Ecol.* (28):347–361. doi:10.1007/BF02515460.
- Miyano S. 1991. Worker reproduction and related behavior in orphan colonies of a Japanese paper wasp, *Polistes jadvigae* (Hymenoptera, Vespidae). *J Ethol.* 9(2):135–46.
- Monnin T, Cini A, Lecat V, Fédérici P, Doums C. 2009. No actual conflict over colony inheritance despite high potential conflict in the social wasp *Polistes dominulus*. *Proc R Soc B.* 276(1662):1593–601.
- Neumann C, Duboscq J, Dubuc C, Ginting A, Irwan AM, Agil M, Widdig A, Engelhardt A. 2011. Assessing dominance hierarchies: validation and advantages of progressive evaluation with Elo-rating. *Anim Behav.* 82(4):911–921.
- Nichols HJ, Bell MBV, Hodge SJ, Cant MA. 2012. Resource limitation moderates the adaptive suppression of subordinate breeding in a cooperatively breeding mongoose. *Behav Ecol.* 23(3):635–642.
- Nonacs P, Hager R. 2011. The past, present and future of reproductive skew theory and experiments. *Biol Rev Camb Philos Soc.* 86:271–298.
- Olson RS, Haley PB, Dyer FC, Adami C. 2015. Exploring the evolution of a trade-off between vigilance and foraging in group-living organisms. *R Soc Open Sci.* 2:150135.
- Page Jr RE, Post DC, Metcalf RA. 1989. Satellite nests, early males, and plasticity of reproductive behavior in a paper wasp. *Am Nat.* 134(5):731–48.
- Pardi L. 1948. Dominance order in polistes wasps. *Physiol Zool.* 21:1–13.
- Ratnieks FL, Foster KR, Wenseleers T. 2006. Conflict resolution in insect societies. *Annu Rev Entomol.* 51:581–608.
- Reeve HK. 1991. *Polistes*. In: Ross KG, Matthews RW, editors. The social biology of wasps. Ithaca (NY): Cornell University Press.
- Reeve HK, Gamboa GJ. 1983. Colony activity integration in primitively eusocial wasps: the role of the queen (*Polistes fuscatus*, Hymenoptera: Vespidae). *Behav Ecol Sociobiol.* 13(1):63–74.
- Reeve HK, Starks PT, Peters JM, Nonacs P. 2000. Genetic support for the evolutionary theory of reproductive transactions in social wasps. *Proc Biol Sci.* 267:75–79.
- Rottler-Hoermann AM, Schulz S, Ayasse M. 2016. Nest wax triggers worker reproduction in the bumblebee *Bombus terrestris*. *R Soc Open Sci.* 3:150599.
- Rubenstein DR. 2012. Family feuds: social competition and sexual conflict in complex societies. *Philos Trans R Soc Lond B Biol Sci.* 367:2304–2313.
- Schindelin J, Arganda-Carreras I, Frise E, Kaynig V, Longair M, Pietzsch T, Preibisch S, Rueden C, Saalfeld S, Schmid B, et al. 2012. Fiji: an open-source platform for biological-image analysis. *Nat Methods.* 9:676–682.
- Schneider CA, Rasband WS, Eliceiri KW. 2012. NIH Image to ImageJ: 25 years of image analysis. *Nat Methods.* 9:671–675.
- Spencer KA, Buchanan KL, Goldsmith AR, Catchpole CK. 2004. Developmental stress, social rank and song complexity in the European starling (*Sturnus vulgaris*). *Proc Biol Sci.* 271 Suppl 3:S121–S123.
- Starks PT, Turillazzi S. 2006. *Polistes* paper wasps: emergence of a model genus. *Ann Zool Fennici.* 43(5–6):385–386.
- Strassmann JE. 1981. Parasitoids, predators, and group size in the paper wasp, *Polistes exclamans*. *Ecology.* 62(5):1225–1233.
- Strassmann JE, Fortunato A, Cervo R, Turillazzi S, Damon JM, Queller DC, Strassmann JE, Queller DC. 2004. The cost of queen loss in the social wasp *Polistes dominulus* (Hymenoptera: Vespidae). *J Kansas Entomol Soc.* 77(4):343–355.
- Strassmann JE, Meyer DC. 1983. Gerontocracy in the social wasp, *Polistes exclamans*. *Anim Behav.* 31(2):431–438.
- Taylor BA, Cini A, Cervo R, Reuter M, Sumner S. 2020. Data from: queen succession conflict in the paper wasp *Polistes dominula* is mitigated by age-based convention. *Behav Ecol.* doi:10.5061/dryad.sf7m0cg31.

- Theraulaz G, Pratte M, Gervet J. 1990. Behavioral profiles in *Polistes dominulus* (Christ) wasp societies: a quantitative study. *Behav.* 113(34):223–250.
- Tibbetts EA, Huang ZY. 2010. The challenge hypothesis in an insect: juvenile hormone increases during reproductive conflict following queen loss in *Polistes* wasps. *Am Nat.* 176:123–130.
- Tibbetts EA, Shorter JR. 2009. How do fighting ability and nest value influence usurpation contests in *Polistes* wasps? *Behav Ecol Sociobiol.* 63(9):1377–1385.
- Tsuji K, Tsuji N. 2005. Why is dominance hierarchy age-related in social insects? The relative longevity hypothesis. *Behav Ecol Sociobiol.* 58(5):517–526.
- Turillazzi S, Pardi L. 1977. Body size and hierarchy in polygynic nests of *Polistes gallicus* (L.) (Hymenoptera Vespidae). *Monit Zool Ital - Ital J Zool.* 11(1–2):101–112.
- Uematsu K, Shimada M, Shibao H. 2013. Juveniles and the elderly defend, the middle-aged escape: division of labour in a social aphid. *Biol Lett.* 9:20121053.
- Viechtbauer W. 2010. Conducting meta-analyses in R with the metafor package. *J Stat Softw.* 36(3):1–48.
- Weiner SA, Noble K, Upton CT, Woods WA, Starks PT. 2011. A role for thermoregulation in the *Polistes dominulus* invasion: a comparison of the thermoregulatory abilities of the invasive wasp *P. dominulus* and the native wasp *P. fuscatus*. *Insectes Soc.* 58(2):185–190.
- West-Eberhard MJ. 1969. The social biology of polistine wasps. *Miscellaneous Pub Museum Zool Univ Michigan* 140(1):1–101.
- Zanette LR, Field J. 2008. Genetic relatedness in early associations of *Polistes dominulus*: from related to unrelated helpers. *Mol Ecol.* 17: 2590–2597.