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SHORT COMMUNICATION

High reproductive skew in the Neotropical paper wasp *Polistes lanio*

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Abstract

Reproductive conflicts are expected in societies where nonbreeding helpers retain the ability to produce offspring. Despite potential competition from reproductively capable nestmates in social wasps, egg laying tends to be monopolised by a single or relatively few queens. Genetic studies on reproductive partitioning in *Polistes* paper wasps suggest high reproductive skew in the genus. Conflict is thought to be minimal due to nestmate relatedness or the possibility of inheriting a reproductive monopoly on a nest; consequently, there are inclusive fitness opportunities for nonreproductive helpers. However, most studies are limited to temperate wasp species. Given the cosmopolitan distribution of *Polistes*, genetic data on group conflicts are required for a broader range of tropical species to determine whether these trends apply across climatic zones. We examined female reproductive skew in the Neotropical paper wasp *Polistes lanio*, genotyping a selection of adults and pupae from established post-emergence nests using single-nucleotide polymorphisms (SNPs). SNP-based pedigree analyses indicate a reproductive monopoly held by a single queen, with queen replacement from natal nestmates and evidence of possible multiple mating. Relatedness between pupal offspring was high ($r = 0.71$). It is likely that high reproductive skew among females is a founding trait of *Polistes* societies, conserved among species that have spread into new environments from Indomalayan origins.

Keywords Reproductive skew · *Polistes* · Single-nucleotide polymorphisms (SNPs) · Pedigrees

Introduction

Societies with many potential breeders must resolve within-group reproductive conflict over who produces young (Clutton-Brock 2009; West et al. 2002). Reproductive skew measures the outcome of such conflict. High reproductive skew is representative of societies in which reproduction is monopolised by a few breeding individuals, whilst low skew is typical of egalitarian societies where reproduction is more equally shared (Ratnieks et al. 2006; Reeve and Keller 2001). When reproduction in a group is limited to a few individuals, there must be a payoff to nonreproductives to continue cooperating (Aureli and de Waal 2000; Hamilton 1964). Revealing social contracts between group members allows the detection of ancestral and derived novel traits within a clade of species.

A reproductive division of labour defines most social insect societies, with a reproducing queen (or sometimes multiple queens) and nonreproductive helpers (workers) who raise the queen's brood. In the eusocial Hymenoptera, helpers can be sterile and unable to reproduce (e.g. honeybees and many species of ants), or totipotent and reproductively suppressed (e.g. *Polistes* paper wasps). The genus *Polistes* includes some of the best-studied species of social wasps, which have proven popular models for testing theories on reproductive partitioning because all group members are reproductively totipotent (to a degree), whether they are functional queens or helping workers (Bell and Sumner 2013; Jandt et al. 2014; West-Eberhard 1969, 1996). Though *Polistes* societies contain many potential reproductives, conflict is expected to be reduced by relatedness among nestmates or the value of inheriting a nest with high reproductive

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skew, respectively, providing indirect and future direct fitness opportunities to nonreproductive helpers (Leadbeater et al. 2011; Queller and Strassmann 1998). Despite *Polistes* being geographically widespread, most genetic studies to date have focused on temperate species (Leadbeater 2011; Liebert 2005; Queller et al. 1997; Reeve et al. 2000; Seppä et al. 2002; Southon et al. 2019). Key differences in the ecologies of temperate and tropical species may alter reproductive opportunities for queens and helpers, for example, tropical species typically have perennial nesting cycles and lack stringent winter diapause, allowing continuous mating opportunities and larger nest structures in terms of both size and membership relative to temperate species (O'Donnell and Joyce 2001; Pickering 1980; West-Eberhard 1969). We lack a broad literature on fine-scale genetic analyses of family structures and reproductive skew among group members of tropical *Polistes* species (Southon 2019). Such genetic-structure data are essential for a proper understanding of potential variation in social organisation, and in how conflicts over reproduction are resolved in the representative early stages of social evolution in a cosmopolitan distributed genus, such as *Polistes* (Bourke 2014).

We genotyped queens, foragers (helpers) and offspring of the Neotropical paper wasp *Polistes lanio* to determine shared parentage and relatedness within established post-emergence nesting groups. *P. lanio* foundresses are pleometrotric; nests are formed by several reproductively capable females who initially compete for dominance (Rusin et al. 2007). Moreover, helpers in this species, like other tropical *Polistes,* appear to retain reproductive potential (e.g. (Sumner et al. 2010; West-Eberhard 1969)); this is because nests can be founded at any time of year, and colonies are asynchronous such that males are always available for mating. As such, most female wasps have the opportunity to become reproductives. Following trends found in multiple species of temperate *Polistes* and in the tropical sister species *Polistes canadensis* (Southon 2019), we predicted that *P. lanio* would exhibit high female reproductive skew indicating queen monopolisation of offspring.

Materials and methods

Ten post-emergence nests were collected from two sites 5.6 km apart in northern Trinidad, Trinidad & Tobago, June 2013 (five nests from Verdant Vale—10°41′5.44″N, 61°17′24.95″W) and August 2014 (five nests from Verdant Vale and Eastern Main Road—10°39′1.21″N, 61°15′9.63″W). Upon collection, nests consisted of a single paper comb, with a mean (± standard error) number of 12.3 ± 2.0 adult females and 111.3 ± 27.6 cells per comb (Supplementary Table S1). Nest membership was recorded at least once per day for 5–22 days by marking individual wasps with honeybee queen tags and Uni POSCA pens. Prior to nest collection, two female behavioural phenotypes were identified: a 'queen', by removal of an egg and observing subsequent oviposition within the day; and a nonreproductive helper 'forager', by observing an individual bringing a solid mass of food back to the nest (in 2013) or by recording which individuals spent the least amount of time on the nest (in 2014). In one nest, a queen could not be identified following egg removal, and so instead the five females who spent the most time on the nest during observations were selected as 'potential queens'. Nest collection occurred at dusk, with adults and brood stored in 80% ethanol at − 20 °C.

The identified queens, a single forager, and a random sample of five pupae were genotyped per nest (24 adults and 50 pupae total). DNA was extracted using a HotSHOT procedure (Montero-Pau et al. 2008; Truett et al. 2000). We used 120 SNP-based markers (KASP™ LGC Genomics) developed for *P. canadensis* and *P. lanio* (see (Southon 2019) for SNP-loci discovery and PCR protocol). First, a subset of 35 pupae (five pupae each from seven nests) were genotyped at all 120 loci. From this subset, monomorphic loci, loci with unclear clustering on a XY plot (MxPro™ Mx3005p® v4.10) and loci with minor allele frequencies < 5% were removed from further analysis (removing 27 loci). All individuals were genotyped, and genetic structure analysed at 93 loci (35 individuals) and 70 loci (39 individuals). Using R 3.3.3 (R Core Team 2013) packages 'adegenet' (Jombart 2008; Jombart and Ahmed 2011), 'genepop' (Rousset 2008) and 'pegas' (Paradis 2010), 10 genotypes (one individual per nest) were assessed at 93 valid loci for deviations from Hardy–Weinberg equilibrium (Bonferroni corrected $\alpha = 0.000538$; 10,000 Monte Carlo permutations) and for linkage disequilibrium (log likelihood-ratio statistic, $\alpha = 0.05$; 1,000 dememorizations; 100 batches; 1000 iterations per batch).

Relatedness was assessed using the Wang (2002) and Lynch and Ritland (1999) metrics in COANCESTRY 1.0.1.8 (Wang 2011), excluding individuals identified as males (pupae with no heterozygous loci). We report relatedness estimates using the Wang estimate, the Lynch & Ritland estimate was used to produce individual inbreeding coefficients (F). A one-sample t-test ($\alpha = 0.05$) was used to determine whether F values deviated from random mating ($F = 0$). SNP-based pedigrees were constructed using COLONY 2.0.6.5 (Jones and Wang 2010) on individuals that had first been sorted into their two respective populations of Verdant Vale and Eastern Main Road (settings: female polygamy, male monogamy, full-likelihood, very long run length, no updated allele frequency, 1% error rate). Though female polygamy is rare in *Polistes*, it was included as low levels of multiple mating have been previously detected in the genus (Seppä et al. 2011; Southon et al. 2019; Strassmann et al. 2001). In the first model, queens and potential queens were designated as possible mothers, with foragers and pupae as offspring. Queens and potential queens with no identified offspring were then designated as offspring in a second model, and these two models combined to construct the complete pedigree. COLONY assignment was accepted if cluster probability p was ≥ 0.8, or if there was ≥ 0.5 probability between the primary and the secondary substructures. To measure reproductive skew between the number of adult females observed on the nest, expressed in genotyped pupae, we calculated the B index which ranges from -1 (equally shared) to 1 (complete skew) (Nonacs 2000) (SKEW CALCULATOR 2003 © Peter Nonacs; settings: 1,000 simulations, 95% CI, $\alpha = 0.05$, equal length of time on nest assumed).

Results

For 93 valid loci, 96.9. ± 0.2% of alleles could be scored successfully across all individuals (see Supplementary Tables S2 & S3). All loci were in Hardy–Weinberg equilibrium (Bonferroni corrected α), with linkage disequilibrium observed across 2.1% of 4,278 pairings ($n = 91$). Mean observed heterozygosity was 0.44 ± 0.02 in Verdant Vale ($n = 8$, $H_{expected} = 0.42 \pm 0.01$) and 0.52 ± 0.04 in Eastern Main Road ($n = 2$, $H_{expected} = 0.33 \pm 0.02$). Mean inbreeding coefficient of all females ($F = -0.03 \pm 0.02$, range -0.27 to 0.34) was not significantly different from zero ($t_{70} = -1.98$, $p = 0.051$), suggesting random mating.

Analyses indicated high levels of reproductive skew, and that presumed low conflict may be attributed to the high nestmate relatedness among adults and/or chance of nest inheritance by daughters (who could alternatively start new nests). A significant female reproductive monopoly was detected across all nests ($B = 0.7191 \pm 0.0124$, $p < 0.05$, range 0.6667–0.7636). Mean relatedness r between female nestmate pupae (overall means of 10 nests, see Supplementary Table S4) was 0.71 ± 0.01 (range 0.64–0.78). Overall mean COLONY assignment probability to pedigree structures was $p = 0.89 \pm 0.05$, range 0.60–1.00. SNP-based pedigree reconstructions revealed six of the nests as having the identified queen as the mother of the forager and pupae (assignment $p = 0.87 \pm 0.08$, range 0.60–1.00; two nests $p < 0.8$ but substructure difference ≥ 0.5; Fig. 1—Panel 2). On three nests, a daughter appears to have replaced (or be attempting to replace) the queen as the identified egg layer but was not the mother to the pupae (assignment $p = 0.97 \pm 0.01$, range 0.95–0.98; Fig. 1—Panel 3). In four nests, an adult offspring had the same mother but a different father to sibling pupae, suggesting some multiple mating (Fig. 1—Panel 2B; Panel 3E/F). One nest had an undetermined pedigree structure, where the queen was assigned as the mother of female pupae and an undetected not genotyped mother as the parent of the forager and a male pupa (assignment $p = 0.78$, substructure difference > 0.5).

Discussion

Although *Polistes* paper wasps have a cosmopolitan distribution, genetic-structure data are critically lacking for tropical species of the genus. This is especially so for data which allow a reconstruction of nesting group genetic structure; for example, most studies on tropical species are based on allozyme data (see Southon et al. 2019). In the Neotropical *P. lanio*, we found that female reproductive skew and between-offspring relatedness in post-emergence nests are on average high. The presence of replacement queens also indicates that natal nests are often inherited by daughters. Both high relatedness and heritable skew in post-emergence nests fit trends found in temperate and tropical *Polistes*.

High reproductive skew is typical in established post-emergence nests of temperate *Polistes* species, suggesting that conflicts over reproduction at this stage in the nesting cycle are relatively resolved. As nonreproducing female helpers (in this study, genotyped foragers) are often offspring of the resident queen and related to the brood, conflict over who reproduces may be reduced as helpers gain indirect fitness from raising siblings (Field et al. 1998; Reeve et al. 2000; Seppä et al. 2002). However, in large nests (R.J.S. pers. obs. of *P. lanio* nests with 60 + adult members present, Trinidad 2015), indirect fitness benefits may become reduced if helper to brood productivity is nonlinear (Grinsted and Field 2018; Nonacs 1991). In our sampled nests, the number of adult females increased linearly with brood number, but bigger nests do have a number of empty cells (see Supplementary Table S1). Brood number may be limited by the queen (fecundity or a monopolisation strategy) or helper productivity. A single genotyped forager was not directly related to the nest pupae may have been a remaining foundress or drifter—a non-natal individual which visits multiple nests (Nonacs 2017). These individuals usually behave as helpers in tropical *Polistes* (Sumner et al. 2007). Whilst nest pupae appear to be mostly related, there may be a potential number of unrelated adults on a nest.

Replacement queens (aka queen turnover) were also detected, often reported in genetic studies as older and younger offspring belonging to different immediate matrilines (Hughes et al. 1987; Peters et al. 1995; Strassmann and Meyer 1983). Given that we detected a high degree of queen replacement among a relatively small sample size, it is likely that queen replacement is a common phenomenon in this species. In complex societies with fixed castes and monopolised reproduction, queen loss may signal the termination of the nesting cycle (Duchateau and Velthuis 1989; Pirk et al. 2004). In simple societies with flexible

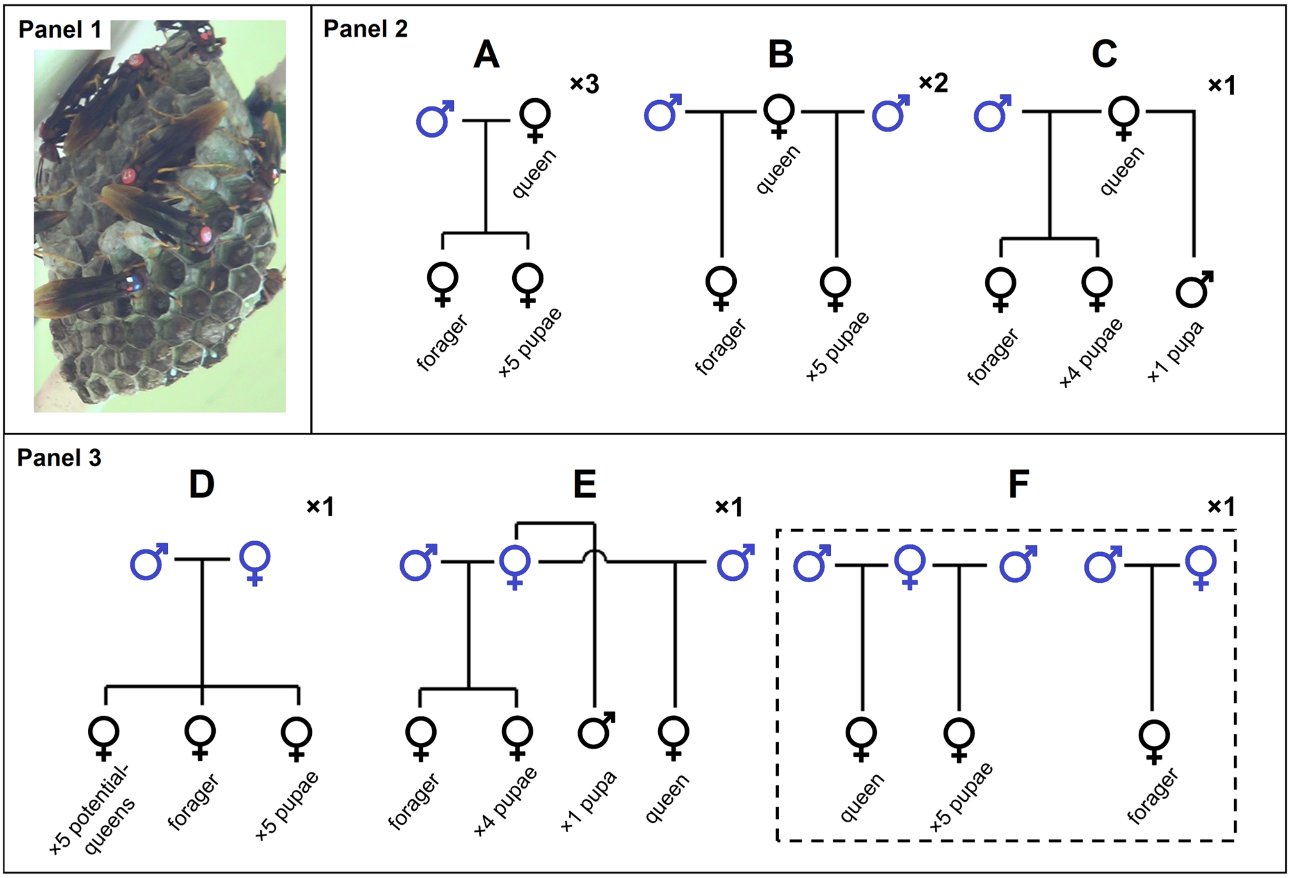

Fig. 1 SNP pedigrees of nine *P. lanio* nests, each pedigree including genotypes (labelled) of an identified queen or potential queens, forager and five pupae (number of nests per pedigree is given in the upper right corner). Panel 1. Post-emergence *P. lanio* nest, in which many female helpers are thought to be capable of becoming queens. Panel 2. Six nest pedigrees in this study had a single queen who monopolised reproduction, with three variates: (A) a singly-mated queen; (B) a twice mated queen, where the sampled forager had a different father but same mother to the pupae; (C) a singly-mated queen, who was the mother to all sampled female and male offspring. Panel 3. Three nests showed pedigrees in which likely queen replacement was observed, with three variates: (D) a singly-mated "queen", not genotyped/detected prior to nest collection, being the mother of all offspring including individuals that showed potential queen-like behaviour (pre- egg laying, sitting around on nests); (E) the mother of female and male offspring was not the queen detected from behaviour observations, which was a half-sister to the other female offspring; (F) two separate matrilines were detected, one was mother to the sampled forager, the other a twice mated mother to the sampled queen and pupae—with a generational split in paternity

helpers, as in *Polistes*, replacement queens may inherit the nest and continue the nesting cycle if there are no seasonal constraints. An alternative explanation for the presence of multiple mothers is that there could occasionally be multiple queens (West-Eberhard 1986).

Multiple mating by the queen was detected in four matrilines, where in each case, two fathers were detected within a single matriline, specifically the adult 'generation' and pupae belonged to separate patrilines. Low levels of multiple mating have sometimes been reported in *Polistes*, including in the sister species *P. canadensis* from analyses with both SNP and microsatellite markers (Southon et al. 2019); however, we cannot rule out the possibility that this could be a miscalculation attributed to how COLONY models novel SNP genotypes. Occurrences of multiple mating and potential re-mating (due to the temporal separation of adult and pupae offspring) warrant further investigation, for example, by genotyping larger numbers of brood across multiple generations through the entire colony cycle. Instances of multiple mating in a species without distinct morphological castes may provide support to the supposition that *Polistes* societies should be viewed more as cooperative breeders than eusocial entities (Boomsma 2009; Boomsma and Gawne 2018), but under what circumstances it arises and ultimately if it has any impact on group social behaviour is unknown.

This study together with the parallel study on its sister species *P. canadensis* (Southon et al. 2019), provides comprehensive genetic evidence that tropical species of *Polistes,* despite differences in ecological conditions, experience similar resolution of reproductive conflict as temperate species. The use of SNP genotyping reveals a range of pedigrees in post-emergence nests although at any one time, there is usually a single, singly-mated mother and her daughters, queen replacement (by daughters) is common and there may be low levels of multiple mating. Such a range of pedigree structures detected within just ten nests (limited to the beginning of the wet season) suggests that relationships in these societies are often complex, and that broader sampling, within and between different times of the season would be important to understand these better. Though general trends in reproductive skew across the genus appear conserved, and it may be presumed that high reproductive skew is an ancestral trait of *Polistes* from its Indomalayan origin (Santos et al. 2015).

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Data availability See provided supplementary files.

Code availability NA.

Conflict of interest None known.

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