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Founders versus joiners: group formation in the paper wasp *Polistes dominulus*

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Within-group power asymmetries and the resulting reproductive skew, common in most social groups, may effectively be set at the very early stages of group formation, that is, when group membership is determined. Hence, groupmate choices can define an individual's future reproductive success. We examined how groups of *Polistes dominulus* formed under natural, unconstrained conditions, using data on the nesting history, kinship and morphology of individually marked foundresses obtained during two consecutive seasons in southern Spain. Foundresses that hibernated in the same aggregation were more likely to start a nest together, but all of the foundresses at a nest were seldom from a single aggregation. Changes in group composition were frequent throughout the preworker period, mainly because some foundresses disappeared and other wasps joined established groups. Within-group relatedness, however, was not affected by the late arrival of wasps. Our results suggest that waiting to join an established group is a common nesting strategy in *P. dominulus*. Only 16% of marked wasps used more than one nest. Foundresses that moved between groups tended to move to groups in which genetic relatedness among the resident foundresses was higher, but not necessarily relatedness to the moving wasp herself. Overall, nestmate choices were not associated with a single factor. High failure rates, particularly of single-foundress nests, however, suggest that ecological constraints (e.g. risk of predation, lack of resources) may have a stronger effect on individual nesting choices than previously considered.

Groups of cooperating individuals are observed from large marine mammals to unicellular amoebae (Strassmann et al. 2000; Mesnick et al. 2003). In most species, individuals form only temporary associations, frequently when breeding or foraging (Wilson 1975; Early & Dugatkin 2010). However, extreme forms of cooperation, in which group members partially or entirely forfeit their reproduction and never leave their natal groups, exist in at least two very distinct groups: vertebrates and insects (Wilson 1971; Reeve 1992; Clutton-Brock 2002). In the aculeate Hymenoptera, in particular, this radical type of cooperation, that is, eusociality, has evolved several times (Wilson 1971; Bourke & Franks 1995). Explaining why individuals sacrifice their own offspring production to assist in the reproduction of others has long puzzled evolutionary biologists (Hamilton 1964; Grafen 1991; Bourke 2011).

Kin selection has provided the major framework for understanding how altruistic behaviours have evolved (Hamilton 1964; Frank 1998). Models based on this theory have made clear predictions about the range of conditions in which cooperative associations should be formed (reviewed in Foster et al. 2006; Lehmann & Keller 2006). Although empirical support for these predictions has been found in many taxa, the focus on within-group reproductive partitioning and relatedness has diverted attention from the process of group formation per se, especially under natural conditions (but see Aron et al. 2009).

Paper wasps of the common temperate species *Polistes dominulus* have a long period of nest foundation (ca. 2 months). Hence, they provide a valuable opportunity to scrutinize the early stages of group formation under natural field conditions. Mated foundresses emerging from their winter diapause refuges in early spring can pursue at least three nesting strategies: nest alone (monogyny), associate with other females forming multiple-foundress nests (polygyny) or remain on their winter refuges and 'sit and wait' to adopt orphaned nests later in the season (Reeve 1991; Starks 2001). Furthermore, before the emergence of workers at the beginning of summer, foundresses may switch groups or usurp established nests, that is, forcibly take the place of others in a group (Reeve 1991).

Potentially, foundresses make crucial behavioural (reproductive) decisions during the preworker period, that is, before dominance is established and group composition is stable. At the beginning and

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end of winter, when temperatures permit, foundresses frequently interact at their winter aggregation sites (Pardi 1942). Interactions range from simple antennation to trophallaxis (exchange of regurgitated food) and dominance interactions (Dapporto et al. 2005). Nevertheless, it remains to be clarified whether wasps that hibernate in the same aggregation are more likely to nest together later.

Once nests are initiated, foundresses are likely to meet exclusively at nests when they attempt to establish new groups or join established ones. Earlier studies indicate that as in other paper wasps, *P. dominulus* foundresses frequently move between nests before worker emergence (reviewed in Reeve 1991; Nonacs & Reeve 1995; Seppa et al. 2002). In seminatural conditions, Pratte (1979) reported that up to 75% of the foundresses switched from their original nest during the first 12 days of the nesting period, visiting on average three nests before settling permanently in a group. It has been suggested that nest-switching foundresses may be assessing the relative reproductive payoffs associated with the available nesting choices (Nonacs & Reeve 1995). Chemical profiles (epicuticular hydrocarbons) can potentially be used to discriminate dominant from subordinate wasps within recently established groups of *P. dominulus* (Sledge et al. 2004). However, foundresses that hibernate in the same winter aggregation have very similar chemical profiles (Dapporto et al. 2004). Thus, additional cues are likely to be used to select individual cofoundresses. Individual variations in body size and colour patterns exist and could potentially be used to select nestmates. Clypeal colour patterns are used in individual recognition by *Polistes fuscatus* females and in the establishment of dominance in *P. dominulus* foundress associations, that is, foundresses with larger and more disrupted clypeal marks tend to be dominants (Tibbetts 2002; Tibbetts & Dale 2004; but see Cervo et al. 2008; Green & Field 2011). However, there is little detailed information on the frequency and magnitude of foundress movements for most paper wasp species (e.g. Seppa et al. 2002; Sumner et al. 2007), so that the generality of these hypotheses remains to be tested.

We analysed the group formation process by examining the nesting histories of individually marked foundresses, and their movement patterns between different groups. We first investigated whether females that hibernate in the same winter aggregations later preferentially found nests together. We then tested the hypothesis that fluctuations in group composition caused by the late arrival of wasps determine intragroup genetic relatedness. Finally, we examined whether foundresses that visit different groups are choosing to join a group according to the kinship structure of the group and within-group variability in body size and facial patterns.

METHODS

Field Data Collection

We carried out field observations and collections at two semirural sites in southwestern Spain (Conil de la Frontera, Province of Cadiz; Site 1: 36°17′11N, 06°04′28W; Site 2: 36°17′11N, 06°03′57W). The habitat at both sites consisted of hedges of prickly pear cactus (invasive *Opuntia* sp., Barbera et al. 1992) surrounded by pasture and crop fields. Hedges were 1.5–3 m high, and 2–21 m wide. Five and four transects, adding up to a total of 500 and 180 m of hedge, were used in Sites 1 and 2, respectively.

Starting on 18 February 2004 and 11 February 2005, we monitored each site every other day (between 1000 and 1400 hours) to locate winter aggregations and newly founded nests. All groups detected were numbered and their locations mapped. On a subsequent day, before wasps were active (0700–0800 hours), females in winter aggregations were marked on the thorax with a large dot of enamel paint, with a unique colour for each aggregation. Wasps were marked directly in the hibernaculum with a long thin brush, since a pilot study showed that when removed from it they did not usually return ($N = 10$ aggregations, 207 wasps marked, three returned). The number of wasps marked in each aggregation depended on its location and size.

All wasps found on new nests were gently collected with long forceps, placed into plastic bags and stored temporarily at 4 °C. Within 4 h of collection, wasps were individually marked (2004: four enamel paint dots; 2005: numbered tags from a honeybee queen marking kit: Thorne, Market Rasen, U.K.) and subsequently released onto their original nests to minimize any possible effect of removal. The proportion of marked wasps that were observed only once (at their original nest) was significantly higher in the second year (0.32 in 2004 and 0.52 in 2005; $\chi^2_1 = 28.963, P < 0.0001$), indicating that the tag marking used in 2005 was more disruptive for the wasps. Marked wasps observed only once at their original marking were not included in our group composition and wasp movement analyses. Wasps marked with numbered tags occasionally lost their tags, but could be identified by the presence of residual glue on the thorax and subsequently re-marked.

Every other day, we inspected all nests in each site early in the morning to detect changes in group composition. All wasps were identified, and newly arrived unmarked wasps were collected, marked and released on the same day.

Wasps that changed nests were placed into three categories: (1) movement with replacement: foundresses that left their initial nest up to 2 days after other foundresses (potential usurpers) arrived; (2) movement without replacement: foundresses that left their initial nest without the arrival of new wasps; and (3) nest-switching foundresses that moved two to three times between the same pair of nests.

Before the first workers started to emerge (May), all remaining marked foundresses and their nests were collected and stored at −80 °C.

Morphological Data Collection

Wings were carefully removed from frozen wasps, unfolded, mounted between glass slides and measured under a 16× Leica binocular microscope. The internal length of the longitudinal cell (Discoidal I) of the right wing was used as a measure of size. Wing length is highly correlated with overall body size (Sullivan & Strassmann 1984).

Wasps' heads were mounted on a glass slide and measured using a 30× Zeiss monocular microscope and the software NIH Image version 1.55 (http://rsbweb.nih.gov/nih-image/). The contour of the black clypeal marks was traced, and the area of the resulting polygon used as an estimate of clypeal mark size.

Genotyping

Total DNA was extracted from the anterior section of the thorax using 300 μl of grinding buffer (0.1 M NaCl; 0.1 M Tris–HCl, $h = 8.0$, 0.05 M EDTA; 0.05% SDS), following Strassmann et al. (1996) with minor modifications. DNA extractions were diluted 1:10 with ultrafiltered distilled water. DNA was extracted from between two and 11 wasps per nest (mean ± SD = 4 ± 2), representing 87% of all foundresses present at collection (mean ± SD = 94 ± 42%).

Multiplex polymerase chain reactions (PCR) were performed using five fluorescently labelled, previously described primer pairs (Pdom 7, Pdom 20, Pdom 127b, Pdom 139, Pdom 140; Henshaw 2000). PCR was carried out using a Peltier Thermal Cycler using 10 μl reactions with 2 μl of DNA sample, 2 μl of reaction buffer ($(NH_4)_2\ SO_2$), 0.6 μl of $MgCl_2$, 0.2 μl of each DNTP, 0.8 μl of each primer and 0.05 μl of Taq polymerase. The PCR products were visualized using an Applied Biosystems 3100 sequencer. Allele sizes