Radio-Tagging Technology Reveals Extreme Nest-Drifting Behavior in a Eusocial Insect

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Summary

Kin-selection theory underlies our basic understanding of social evolution [1, 2]. Nest drifting in eusocial insects (where workers move between nests) presents a challenge to this paradigm, since a worker should remain as a helper on her natal colony, rather than visit other colonies to which she is less closely related. Here we reveal nest drifting as a strategy by which workers may maximize their indirect fitness by helping on several related nests, preferring those where the marginal return from their help is greatest. By using a novel monitoring technique, radio frequency identification (RFID) tagging, we provide the first accurate estimate of drifting in a eusocial insect: 56% of females drifted in a natural population of the eusocial paper wasp Polistes canadensis, exceeding previous records of drifting in natural populations by more than 30-fold. We demonstrate that drifting cannot be explained through social parasitism, queen succession, mistakes in nest identity, or methodological bias. Instead, workers appear to gain indirect fitness benefits by helping on several related colonies in a viscous population structure. The potential importance of this strategy as a component of the kin-selected benefits for a social insect worker has previously been overlooked because of methodological difficulties in quantifying and studying drifting.

Results and Discussion

In groups of related individuals, group members may gain fitness benefits (b) by helping raising closely related young (of relatedness r) at the cost (c) of sacrificing their own direct reproduction, such that altruistic behavior is selected for when rb > c [1]. In the Hymenoptera (bees, wasps, and ants), females are more closely related to their sisters (r = 0.75) than to their own offspring (r = 0.5) because of their haplodiploid genetic sex-determination system. Females are therefore selected to become altruists (workers) on their natal colony [2]. Despite these predictions, nest drifting has been reported among the eusocial Hymenoptera (e.g., polistine wasps [3–6], vespine wasps [7], bumblebees [8, 9], and honeybees [10–15]). However, the importance of drifting behavior and its implications for kin-selection theory are poorly understood because of the difficulties in studying it, especially in natural populations (see Table 1).

We used radio frequency identification tags (RFID) to quantify nest drifting in a natural population of the primitively eusocial wasp Polistes canadensis in Panama. Passive RFID tags bearing unique identification numbers can be attached to the thorax of an insect, such that the identity is recorded each time insects pass antennae fixed at nest entrances [16]. This provides continuous real-time data on the movement of individuals between nests over extended time periods, which is much less labor intensive than traditional marking techniques. Queen and worker roles in primitively eusocial insects are facultative such that all females have the potential to become egg-layers (queens). Females therefore can choose whether to remain at their natal nest as a worker, cofound a new colony, or join another nest as a worker or potential egg layer [17]. The reproductive options are especially flexible for tropical species such as P. canadensis where there is no fixed end to the colony cycle [18]. Based on their colony genetic structure, kin-selection theory predicts that P. canadensis workers should not engage in drifting behavior because female nest mates are closely related (r = 0.47 ± 0.049; n = 28 nests, 145 wasps). They should remain faithful to their natal nests where the indirect fitness benefits of helping are high.

Contrary to this prediction, we found extreme levels of nest drifting in P. canadensis. Of the 422 tagged wasps, 157 were recorded twice or more, and 88 (56.1%) of these were recorded visiting multiple nests (i.e., drifting). True drift rate is likely to be higher because not all nests in the population were monitored. Drifting was detected on 31 of the 33 (94%) monitored nests. Pairs of nests shared up to 54.5% of their wasps. Drifters were observed on 2–21 occasions (mean = 7.8 ± 0.45) and visited between 2 and 5 nests, with 59% of drifters visiting 2 nests (Figure 1). A model of wasp behavior (see Experimental Procedures) suggests that drifters were on average twice as detectable as nondrifters (probability of detection per day: 0.50 versus 0.27). After accounting for this, the minimum estimate of drifting in the population (D*) was 39.5%. This is 31 times higher than any previous record of drifting in a natural population of a eusocial insect [12] and 8–10 times higher than drifting rates recorded in artificial populations of honeybees where hives had been arranged to encourage drifting [11] (Table 1). The high drift rate we observed in P. canadensis therefore invokes new questions on the ecological and evolutionary

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significance of this behavior. We tested the key hypotheses that might explain drifting behavior.

**Hypothesis 1: Drifting Is an Artifact of the Technique and/or Study Population**

Drifting may be an artifact if individuals became disoriented as a result of tagging. In our study, all females on disturbed colonies were tagged. Thus, if drifting were an artifact of tagging, we would expect relatedness of untagged females on colonies that were not disturbed to be significantly higher than that of females on colonies that were disturbed. We found no evidence for this (Table 2; \( t = -0.24, p = 0.84 \)). Moreover, drifting is not an artifact of the study population or field season, because it occurred in consecutive years with different methods. The previous year, 10.6% of paint-marked females were detected drifting at the same site, and 8.9% of females drifted in a second population 5 km away (Table 1).

Strikingly, the drift rates obtained through traditional census techniques are 5-fold less than those revealed from the radio-tagging data (Table 1). The main reason for this difference is the intensity with which the different methods collect data. The radio-tagging data collected in 2005 represent nearly 6000 observation hours, compared with around 100 hours with paint-marking in 2004. Based on 2% of the available data, we estimate the rate of drifting at around 25% (based on 500 random samples). Any remaining discrepancy can be explained by differences in the way wasps are recorded: a traditional census represents a snapshot of those present on the nest, whereas radio-tagging records the movement of wasps as they arrive and leave. Thus, traditional methods are inferior to RFID methods unless all nests can be watched continuously for an equivalent amount of time. Drifting estimates obtained by genotyping nestmates (see Table 1) will likewise underestimate drifting because sampling represents a single time point. Given

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**Table 1. Comparison of Drift Rate in Eusocial Insects**

<table>
<thead>
<tr>
<th>Species (Study)</th>
<th>Method</th>
<th>Study Type</th>
<th>Drift Rate</th>
<th>Number of Females; Number of Nests</th>
<th>Drifting Explanation</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. canadensis</em> (this study)</td>
<td>RFID tags</td>
<td>natural</td>
<td>40–56</td>
<td>422; 33</td>
<td>indirect fitness</td>
</tr>
<tr>
<td><em>P. canadensis</em> (2004 data)</td>
<td>paint</td>
<td>natural</td>
<td>10.6</td>
<td>584; 37</td>
<td>n/a</td>
</tr>
<tr>
<td><em>P. canadensis</em> (2004 data)</td>
<td>numbers and paint</td>
<td>natural</td>
<td>8.9</td>
<td>806; 26</td>
<td>n/a</td>
</tr>
<tr>
<td><em>Apis mellifera capensis</em> [11]</td>
<td>paint</td>
<td>wild caught; artificial2</td>
<td>4.8</td>
<td>12,034; 36</td>
<td>social parasitism</td>
</tr>
<tr>
<td><em>Apis mellifera carnica</em> [13]</td>
<td>numbers</td>
<td>artificial2</td>
<td>13–39</td>
<td>200; 12</td>
<td>artefact/accidental</td>
</tr>
<tr>
<td><em>Apis mellifera carnica</em> [10]</td>
<td>worker genotypes</td>
<td>artificial3</td>
<td>5.0</td>
<td>1359; 38</td>
<td>n/a</td>
</tr>
<tr>
<td><em>Apis dorsata</em> [12]</td>
<td>worker genotypes</td>
<td>natural</td>
<td>1.3</td>
<td>1537; 24</td>
<td>n/a</td>
</tr>
<tr>
<td><em>Apis florae</em> [15]</td>
<td>worker and brood genotypes</td>
<td>wild caught; translocated</td>
<td>2.0</td>
<td>392; 4</td>
<td>social parasitism</td>
</tr>
<tr>
<td><em>Bombus terrestris</em> [9]</td>
<td>brood genotypes</td>
<td>wild caught; artificial</td>
<td>174</td>
<td>2,500; 32</td>
<td>social parasitism</td>
</tr>
</tbody>
</table>

Drift rate is defined as the percentage of workers observed on multiple nests. Only studies where quantitative measures of drifting are available were included in this summary. Methods used include radio-tagging ("RFID tags"), paint-marking ("paint"), tagging with numbers ("numbers"), and genotyping either brood (in order to detect nonnestmate eggs) or workers (to detect nonnestmates).

1 Alternate study site.
2 Colony set-up designed to encourage drifting.
3 Colony set-up designed to discourage drifting.
4 C. Lopez-Vaamonde, personal communication.

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**Figure 1. Histogram of Observation Frequency and Number of Nests Visited for 187 Tagged Wasps**

Observation frequency is defined as number of wasps. Drifters are those wasps recorded on more than one nest.
In the honeybee and bumblebee, drifting workers socially parasitize the nests they visit by laying male eggs but contributing nothing else to colony resources or management [7–9, 11]. If *P. canadensis* drifters were social parasites, they would have mature eggs in their ovaries and may also be mated (i.e., able to lay haploid male eggs as well as diploid female eggs). Of the 18 *P. canadensis* drifters collected at the end of the monitoring period, 14 were inseminated but none had developing or mature eggs in their ovaries. *P. canadensis* drifters therefore are not actively engaged in egg laying on the nests they visit, indicating that drifting is not a strategy for social parasitism in this species (hypothesis 3).

Drifting may be a strategy by which females assess future opportunities for egg laying on nonnatal colonies (hypothesis 4). Queuing as a hopeful reproductive or usurping an existing queen are common alternative reproductive strategies in primitively eusocial insects, where all females have the reproductive potential to lay eggs [17]. If drifters were attempting to become queens on the nests they visit, then drifting would be a temporary strategy, after which drifters settle as egg layers on a single nest. Yet the majority of wasps show no change-point in their drift rate, suggesting that drifting is generally a permanent strategy. Specifically, 23% of drifters accumulated more nests at the start of the monitoring period than at the end, as expected under sampling if drift rate does not change over time. If drifting were a temporary strategy, some females would be expected to start drifting during the monitoring period, yet none did. Moreover, 78% of drifters showed no significant change in drift rate over the monitoring period, suggesting that they were drifting permanently. These analyses suggest that the majority of drifters’ behavior remained constant for the entire 4-week monitoring period and that drifting is therefore not a temporary strategy.

If drifters were attempting to become queens on the nests they visit, we would expect them to be young females. This is because caste plasticity in tropical polistine wasps appears to decline with age such that only young females are able to compete socially for reproductive dominance [20, 21] (*P. canadensis*: S.S., unpublished data). The age range of drifters was not restricted to young females (range = 4–58 days; n = 58 drifters; data from paint-marked females 2004 marked on emergence), suggesting that drifting is not an age-determined strategy. In conclusion, we found no evidence that drifters are visiting nests in order to attempt becoming future egg layers.

### Hypothesis 5: Drifters Gain Indirect Fitness Benefits

Drifters may be gaining indirect fitness benefits by helping raise brood on several related colonies. Behavioral observations indicate that drifters behave like workers rather than queens in the rate at which they perform caste-diagnostic behaviors on the nests they visit (Figure 2; drifter versus worker behaviors, $\chi^2_{(52,112)} = 1.67$, $p = 0.2$; drifter versus queen behaviors, $\chi^2_{(118,24)} = 23.5$, $p < 0.0001$). Moreover, there was no significant difference in the rate at which drifters performed queen or worker tasks on their main (i.e., most-visited) nest and secondary nests (worker behaviors on main versus secondary nest, $\chi^2_{(52,26)} = 0.94$, $p = 0.33$; queen behaviors on

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**Table 2. Relatedness Estimates ± Standard Errors for Adult Females and Drifters to Adults and Eggs in Their Natal Nests, Nests in Drifter Groups, and Nests Not in Drifter Groups**

<table>
<thead>
<tr>
<th>Group</th>
<th>Adults</th>
<th>Eggs</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Adult females</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Within untagged nests</td>
<td>0.47 ± 0.096 (5)</td>
<td>na/a</td>
</tr>
<tr>
<td>Within tagged nests</td>
<td>0.46 ± 0.049 (28)</td>
<td>0.34 ± 0.063 (15)</td>
</tr>
<tr>
<td>Drifter group</td>
<td>0.22 ± 0.057 (14)</td>
<td>0.11 ± 0.044 (12)</td>
</tr>
<tr>
<td>Non-drifter group</td>
<td>−0.0066 ± 0.015 (14)</td>
<td>0.018 ± 0.018 (14)</td>
</tr>
<tr>
<td><strong>Drifters</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Natal nest</td>
<td>0.5 ± 0.195 (4)</td>
<td>0.56 ± 0.135 (2)</td>
</tr>
<tr>
<td>Drifter group</td>
<td>0.26 ± 0.079 (14)</td>
<td>0.19 ± 0.049 (12)</td>
</tr>
<tr>
<td>Drifter group, excluding natal</td>
<td>0.25 ± 0.083 (8)</td>
<td>0.19 ± 0.071 (8)</td>
</tr>
<tr>
<td>Non-drifter group</td>
<td>−0.012 ± 0.02 (14)</td>
<td>0.022 ± 0.02 (14)</td>
</tr>
</tbody>
</table>

Sample sizes of nests are given in parentheses: for drifter groups/nondrifter groups, samples sizes are the number of drifter groups rather than number of individual nests.

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**Hypothesis 2: Drifters Make Mistakes in Nest Identity**

Accidental nest drifting by workers occurs in apiaries and greenhouses where colony densities are artificially inflated [11, 13]. If *P. canadensis* drifters were making mistakes in nest identity, we would expect them to visit nests randomly with regard to relatedness and nonrandomly with regard to geographic proximity, because females are most likely to visit nearby nests by accident than those far away. We found that drifters visit nests to which they are closely related, suggesting that drifting is not random with respect to relatedness: drifters were more closely related to the adults on nests that they visited (drifter groups) than those on nests they did not visit (nondrifter groups) (*Table 2; t = 3.39, p = 0.005*). Drifters were more likely to visit nearby nests (Mantel test, $r = −0.442$, $p < 0.001$), although only 50 of the 100 closest pairs of nests (all within 6.7 meters of one another) shared any wasps, and six pairs of nests shared wasps in spite of being more than 40 meters apart. These findings are likely to be a product of the population structure rather than an indication that drifting is accidental. Nest founding in primitively eusocial insects often occurs through colony fission whereby new nests are founded nearby the parent nest by groups of sisters [4, 19], providing the basis for high genetic population viscosity. Our data support this: wasps on neighboring nests tend to be closely related (Mantel test, $r = −0.138$, $p < 0.05$). Moreover, wasp relatedness within drifter groups is significantly higher than relatedness within nondrifter groups (*Table 2; t = −3.76, p = 0.002*). Drifting, therefore, is unlikely to be accidental, but instead occurs within extended colonies.

**Hypotheses 3–4: Drifters Gain Direct Fitness Benefits**

Drifting behavior may be selected for if drifters are laying eggs on the nests they visit, either as social parasites (hypothesis 3) or as future queens (hypothesis 4).
were, on average, smaller than their natal nest (binomial
that 19/22 newly emerged drifters visited nests that
nests where their help is worth more. Indeed, we find
[20, 21], so drifters might be expected to drift to small
function of colony size in primitively eusocial insects
[i.e., the increase in reproductive output resulting from
this case refers to the colony’s marginal productivity
other component is the benefit of cooperation, which in
workers maximize their inclusive fitness by reducing the
risk that all their investment is lost through whole-nest
predation. A similar strategy has been reported in sub-
tropical Polistes, where workers and queens rear brood
in both mother and satellite nests [4]. Risk-spreading
strategies are common among organisms living in vari-
ble environments, for example in desert insects that re-
main dormant for a year in order to avoid the effects of
an unpredictable drought [23] and in insects that lay
their eggs on several host plants even though one plant
has ample resources to support an entire clutch [24].

Conclusions
Two key conditions are likely to have facilitated the evo-
lution of drifting for indirect fitness benefits: an unpre-
dictable environment and a population consisting of
extended colonies. Helping on several related nests
has not previously been recognized as a strategy by
which workers may maximize inclusive fitness. Consid-
eration of any indirect fitness achieved on nonnatal
nests may account for cases where kin-selection theory
has failed to explain the evolution of helping behavior
[25]. The potential importance of drifting behavior as an
alternative reproductive strategy, and its implications
for kin-selection theory, have previously been over-
looked because of the difficulties in quantifying drifting.

Experimental Procedures
The site consisted of a population of P. canadensis paper wasps
nesting under three wooden buildings at Hospital National Estancia
Larga, Republic of Panama (8° 54′ 44″ N, 79° 33′ 47″ W). All small and
medium sized nests accessible under these three buildings were
used in the study. Seven nests were pre-emergence colonies, on
which the first adults had not yet emerged (mean number of cells = 19 ± 4.2; mean number of females = 4.0 ± 0.65). The remaining
20 were postemergence colonies (mean number of cells = 175 ± 26; mean number of females = 19.7 ± 2.6).

Quantification of Drifting via Radio Frequency
Identification Tags
All wasps were collected before dawn between 4 and 12 June 2005.
Radio frequency identification tags (passive RFID, 16 bit program-
ming mode [GISQ5Bee Tags], 18 mg < 1% body mass of a typical
test, p < 0.001). However, any increase in productivity
must be large to offset the lower relatedness of drifters
to nonnatal nests (Table 2). Therefore, it is likely that
drifting is a costly strategy in P. canadensis. The high
levels of drifting we observed imply that the costs of not
drifting outweigh the genetic benefits. A likely cost
is whole-nest predation, whereby all brood within
a nest are destroyed, usually by birds or ants, but where
adult wasps remain unharmed. This form of predation is
common in Polistine wasps, particularly in the tropics
[22], and has a substantial influence on brood survivor-
ship relative to other forms of brood loss (e.g., parasit-
oids and disease) where only one or a few individual
brood per nest are destroyed [22]. By helping raise rel-
ated brood on several nests, drifters could increase
the chance that at least some of their investment is pre-
served in the face of whole-nest predation. Whole-nest
predation rate in our radio-tagged population was
high, such that an egg has a 40% chance of being eaten
by a whole-nest predator before reaching adulthood
(n = 84 nests; brood development time = 42 days). Drift-
ing may therefore be a risk-spreading strategy whereby
workers maximize their inclusive fitness by reducing the
risk that all their investment is lost through whole-nest
predation.

Figure 2. Comparison of the Rates of Queen and Worker Behaviors
Performed by Drifters
See Experimental Procedures for behaviors analyzed (**p < 0.001; *p < 0.05).
P. canadensis female, 6 × 2 mm) encoded with unique 4-digit identification numbers were glued to the thorax of each collected wasp (Locitite). In total, 423 wasps were tagged from the 27 nests. Any newly emerged females (with black eyes, n = 69) that were tagged were placed back on their nests with forceps in order that they could orientate from their natal nest. All other tagged females were released near their nests and watched in order to verify that they could fly well. The entrance to each nest was restricted to a 20 × 20 cm entrance hole by means of fine netting, and a circular antenna (3 cm diameter, GiS TS-A37) was attached 10 cm in front of the nest in the center of the entrance. Each antenna was connected to a scanner (GiS TS-R64; powered by 12V battery) where the time, date, and identification numbers of each wasp detected by the antenna was stored. This arrangement minimized disturbance to the wasps and enabled most wasps that entered or left the nest to be detected. Drifting to larger nests was monitored by placing 2 to 4 scanners on each of six large nests (mean number of cells = 510 ± 39; number of females > 200) on which wasps were not tagged. Data from the scanners on each large nest were combined. In total, movements of wasps between 33 nests were monitored. Scanners were activated after dawn each day, recording wasp movements for an average of 0.61 ± 0.30 hr per day for 21 days, over a period of 4 weeks (June 16, 2005, to July 13, 2005). All brood and adult wasps present at the end of the monitoring period were collected after dark and frozen for DNA analysis. All collected drifters were dissected to assess their ovarian development and determine whether there was sperm present in their spermathecae.

Any wasp that was recorded visiting more than one nest during the monitoring period was defined as a drifter. Drift rates in P. canadensis obtained from RFID data were compared with those obtained with traditional census techniques at the same site in the previous year (20 census records of 584 paint-marked females, 37 nests, taken every 2 days over 6 weeks [May–July]) and at a site 5 km away (24 census records of 806 paint-marked/numbered females, 26 nests, taken every 2 days over 7 weeks [May–July]). In each case, drift rate was estimated as the number of marked females recorded after marking that were seen on two or more nests as a proportion of total wasps recorded more than once.

Behavioral Observations
We observed the rate at which queen behaviors (giving aggression, new cell construction, egg laying, and abdomen wagging) and worker behaviors (foraging, receiving aggression) were performed by 33 drifters on 15 nests over 18 hr. Count data on the rate of task performance were standardized for an average wasp (untagged or tagged nondrifters) on that nest, and compared with equivalent data from a previous study at the same site (12 queens and 80 workers from 12 nests; S.S., unpublished data).

Molecular Analyses
All collected drifters, 5 untagged females from each nest (n = 28) and 5–8 female eggs per nest were genotyped at 6 polymorphic microsatellite loci under standard conditions (7–11 alleles per locus; Pan109, Pan117, Pan63, Pan93, Pan120, Pbe411 [26]). Relatedness was estimated in Relatedness 5.0.7, jackknifed over nests [27].

Statistical Analyses
To estimate the proportion of drifters, the population of tagged wasps was modeled as a multistate phenomenon with Program MARK [28]. For this and subsequent analyses, we included only one observation of each wasp per nest per day (n = 1037, excluding the occasions on which wasps were tagged). All individuals were initially coded as nondrifters and were considered drifters once they were recorded on two different nests. Thus, we assume that drifters do not return to the nondrifter state (tested in hypothesis 4). The transition rate at which nondrifters become drifters was estimated, and survival and detection probabilities for drifters and nondrifters were modeled separately (as in a conventional capture-recapture model). Thus, the rate of change in the number of drifters is given by the difference in the rates of drifting and mortality (of drifters); the rate of change in the number of nondrifters is given by recruitment minus drifting and mortality (of nondrifters). At equilibrium, when (total) mortality and recruitment are equal, the proportion of drifters in the population is given by D = d/(d + m), where d is the rate at which nondrifters become drifters, and m is the mortality rate. To estimate these parameters, we compared the fit of competing models with AIC. We found that the mortality rate of drifters and nondrifters did not differ (m = 0.070 per wasp per day), and the rate at which nondrifters became drifters was 0.046 per wasp per day. Detection probabilities varied among days (probably because of weather conditions) but were consistently and significantly higher for drifters than nondrifters (mean = 0.50 versus 0.27). We compared the observed frequency distribution of drifters on different nests with that expected under a null model in which the number of visits is spread randomly among all the nests visited. To do this, the probability density of the observed distribution was calculated under a multinomial distribution separately for each wasp that was observed on at least three occasions (n = 63 drifters), and combined with the unweighted Z-transformation [29].

If drifting were a temporary strategy, we would expect some females to stop drifting and others to start. To test this, each record of a drifter was coded according to (1) whether the observation was on an entirely new nest and (2) whether the observation was on a different nest from the previous observation. Thus, two data sets were generated for each drifter and analyzed with change-point statistics [30] to detect individuals that switch from a nondrifting to a drifting behavior (and vice versa) during the study period. If drifting were a permanent state, the probability of being seen on a new nest is predicted to show change-points from high at the start of monitoring (through sampling) to low at the end (once all the nests in a “drifter group” have been recorded). The converse is expected if drifting were a temporary strategy. Change points in the probability that sequential observations are on different nests would indicate drifting were a temporary strategy.

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