Report

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

Seirian Sumner,[1,*] Eric Lucas,[1,2] Jessie Barker,[1,3] and Nick Isaac[1]
[1] Institute of Zoology
Zoological Society of London
Regent's Park
London NW1 4RY
United Kingdom
[2] Department of Biology
University College London
Wolfson House
4 Stephenson Way
London NW1 2HE
United Kingdom
[3] Department of Neurobiology and Behavior
Cornell University
Ithaca, New York 14853

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

*Correspondence: seirian.sumner@ioz.ac.uk

Table 1. Comparison of Drift Rate in Eusocial Insects

Species (Study)	Method	Study Type	Drift Rate	Number of Females; Number of Nests	Drifting Explanation
P. canadensis (this study)	RFID tags	natural	40–56	422; 33	indirect fitness
P. canadensis (2004 data)	paint	natural	10.6	584; 37	n/a
P. canadensis (2004 data)[1]	numbers and paint	natural	8.9	806; 26	n/a
Apis mellifera capensis [11]	paint	wild caught; artifical[2]	4.8	12,034; 36	social parasitism
Apis mellifera carnica [13]	numbers	artifical[2]	13–39	200; 12	artefact/accidental
Apis mellifera carnica [10]	worker genotypes	artifical[3]	5.0	1359; 38	n/a
Apis dorsata [12]	worker genotypes	natural	1.3	1537; 24	n/a
Apis florae [15]	worker and brood genotypes	wild caught; translocated	2.0	392; 4	social parasitism
Bombus terrestris [9]	brood genotypes	wild caught; artificial	17[4]	2,500; 32	social parasitism

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.

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 disorientated 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
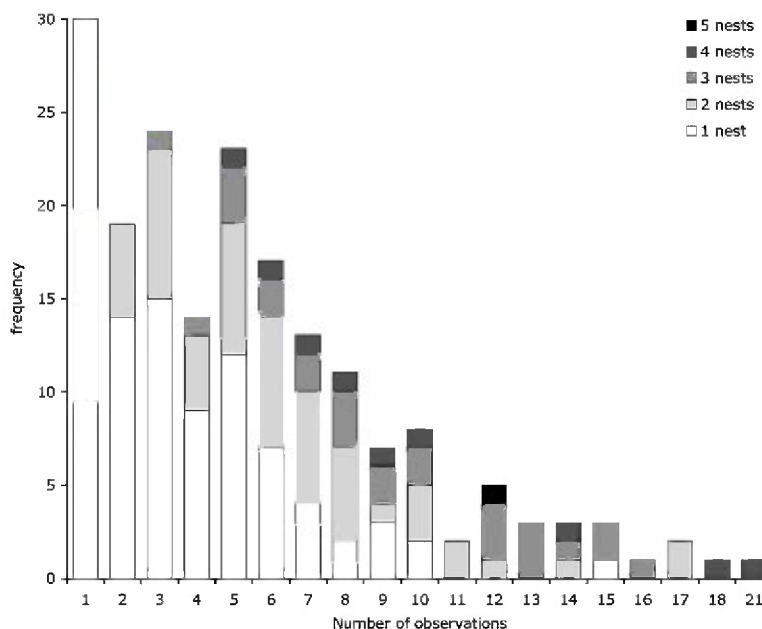

Figure 1. Histogram of Observation Frequency and Number of Nests Visited for 187 Tagged Wasps

Observation frequency is defined as number of wasps. Drifters are those wasps recorded on more than one nest.

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

Group	Adults	Eggs
Adult females		
Within untagged nests	0.47 ± 0.096 (5)	n/a
Within tagged nests	0.46 ± 0.049 (28)	0.34 ± 0.063 (15)
Drifter group	0.22 ± 0.057 (14)	0.11 ± 0.044 (12)
Nondrifter group	−0.0066 ± 0.015 (14)	0.018 ± 0.018 (14)
Drifters		
Natal nest	0.5 ± 0.195 (4)	0.56 ± 0.135 (2)
Drifter group	0.26 ± 0.079 (14)	0.19 ± 0.049 (12)
Drifter group, excluding natal	0.25 ± 0.083 (8)	0.19 ± 0.071 (8)
Nondrifter group	−0.012 ± 0.02 (14)	0.022 ± 0.021 (14)

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.

these methodological considerations, the drift rates previously reported for eusocial insects are likely to be underestimates, and drifting is likely to be more widespread than perceived to date (see Table 1).

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).

In the honeybee and bumblebee, drifting workers socially parasitise 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, $\chi^2_{(52,28)}$ = 0.94, p = 0.33; queen behaviors on
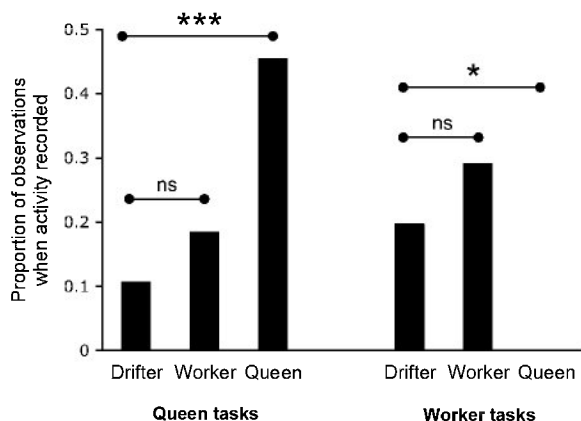
Figure 2. Comparison of the Rates of Queen and Worker Behaviors Performed by Drifters

See Experimental Procedures for behaviors analyzed (***p < 0.001; *p < 0.05).

main versus secondary nest, $\chi^2_{(104,56)}$ = 0.25; p = 0.62). These results suggest that drifters are workers who help raise brood on the nests they visit and that their behaviors are similar on all nests.

Next, we quantified any indirect fitness that drifters may achieve by helping on the nests they visit. Drifters were more closely related to the nests they visited than to the nests they did not visit (Table 2; eggs, t = 2.34, p = 0.037; adults, t = 3.39, p = 0.0047), indicating that drifters have the potential to gain indirect fitness by helping on the nests that they visit. However, drifters are likely to gain higher indirect fitness by helping on their natal nest rather than by helping on secondary nests (r(drifters to natal adults and brood) = 0.52 ± 0.12 (n = 6 nests); r(drifters to adults and brood visited, excluding natal nest) = 0.23 ± 0.056 (n = 9 nests); t = −2.49; p = 0.040).

Drifters may be apportioning helping effort in relation to the relative indirect fitness they can achieve from the different nests in their drifter group. A multinomial test revealed that the distribution of visitation rate among nests was much less even than if wasps moved randomly among the nests they visited (Z = −12.34, p < 0.0001). This indicates that drifters tend to visit some nests more than others. Drifters apportioned between 33% and 94% of their visits to the main nest (mean = 72.8% ± 14.8%), and half (51%) of the drifters were recorded at least twice on a secondary nest. Of the 22 newly emerged drifters, 18 (82%) main nests were their natal nests, suggesting that drifters invest the most help in the nest to which they gain the greatest indirect fitness return.

Thus far, we have considered only one component of Hamiltonian indirect fitness [1], namely relatedness. The other component is the benefit of cooperation, which in this case refers to the colony's marginal productivity (i.e., the increase in reproductive output resulting from drifting). Colony productivity per worker is a negative function of colony size in primitively eusocial insects [20, 21], so drifters might be expected to drift to small nests where their help is worth more. Indeed, we find that 19/22 newly emerged drifters visited nests that were, on average, smaller than their natal nest (binomial

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 survivorship relative to other forms of brood loss (e.g., parasitoids and disease) where only one or a few individual brood per nest are destroyed [22]. By helping raise related brood on several nests, drifters could increase the chance that at least some of their investment is preserved 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). Drifting 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. A similar strategy has been reported in subtropical *Polistes*, where workers and queens rear brood in both mother and satellite nests [4]. Risk-spreading strategies are common among organisms living in variable environments, for example in desert insects that remain 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 evolution of drifting for indirect fitness benefits: an unpredictable 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. Consideration 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 overlooked because of the difficulties in quantifying drifting.

P. canadensis female], 6 × 2 mm) encoded with unique 4-digit iden-
tification numbers were glued to the thorax of each collected wasp
(Loctite). In total, 422 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 re-
leased 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 an-
tenna 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 8.61 ± 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 af-
ter dark and frozen for DNA analysis. All collected drifters were dis-
sected 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. canaden-
sis* 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 micro-
satellite loci under standard conditions (7–11 alleles per locus;
Pan109, Pan117, Pan63, Pan93, Pan120, Pbe411 [26]). Relatedness
was estimated in Relatedness 5.0.7, jacknifed over nests [27].

Statistical Analyses
To estimate the true 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 revert 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 cap-
ture-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 equi-
librium, when (total) mortality and recruitment are equal, the pro-
portion 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 signifi-
cantly higher for drifters than nondrifters (mean = 0.50 versus 0.27).

We compare 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 = 83 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 dif-
ferent 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 switched 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 pre-
dicted 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 se-
quential observations are on different nests would indicate drifting
were a temporary strategy.

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