



Copy when uncertain: lower light levels increase trail pheromone depositing and reliance on pheromone trails in ants

Sam Jones^a, Tomer J. Czaczkes^{b,*}, Alan J. Gallager^a, Felix B. Oberhauser^b, Ewan Gourlay^c, Jonathan P. Bacon^a

^a School of Life Sciences, University of Sussex, Brighton, U.K.

^b Department of Zoology and Evolutionary Biology, University of Regensburg, Regensburg, Germany

^c Brighton and Sussex Medical School, University of Sussex, Brighton, U.K.

ARTICLE INFO

Article history:

Received 21 November 2018

Initial acceptance 14 January 2019

Final acceptance 17 July 2019

Available online 14 September 2019

MS. number: 18-00832R

Keywords:

ants
information conflict
information use strategies
light levels
pheromone depositing
route learning

Animals may gather information from multiple sources, and these information sources may conflict. Theory predicts that, all else being equal, reliance on a particular information source will depend on its information content relative to other sources. Information conflicts are a good area in which to test such predictions. Social insects, such as ants, make extensive use of both private information (e.g. visual route memories) and social information (e.g. pheromone trails) when attempting to locate a food source. Importantly, eusocial insects collaborate on food retrieval, so both information use and information provision may be expected to vary with the information content of alternative information sources. Many ants, such as *Lasius niger*, are active both day and night. Variation in light levels represents an ecologically important change in the information content of visually acquired route information. Here, we examined information use and information provision under high light levels, equivalent to a bright but overcast day, moderate light levels, simulating dusk, and darkness, equivalent to a moonless night. Ants learned poorly, or not at all, in darkness. As light levels decreased, ants showed decreasing reliance on private visual information, and a stronger reliance on social information, consistent with a ‘copy when uncertain’ strategy. In moderate light levels and darkness, pheromone depositing increased, presumably to compensate for the low information content of visual information. Varying light levels for cathemeral animals provides a powerful and ecologically meaningful method for examining information use and provision under varying levels of information content.

Crown Copyright © 2019 Published by Elsevier Ltd on behalf of The Association for the Study of Animal Behaviour. All rights reserved.

Strategic information use is critical to the success of many animals. Animals must, for example, decide whether to explore new options, exploit the knowledge they already have, or use information gleaned from or sent by other animals about potential options (Grüter & Leadbeater, 2014; Laland, 2004; Leadbeater & Dawson, 2017). Two important classes of information for animals are private information and social information. Private information sources cannot be accessed by others, and include genetic information, internal states and, importantly, memories. Social information is information gathered from observation of, or interaction with, other animals or their products (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005; Heyes, 1994). These may be cues,

such as indications of conspecifics having recently been in a particular location (Worden & Papaj, 2005; Wüst & Menzel, 2017), or intentionally produced social signals, such as the waggle dance of honey bees or pheromone trails deposited by ants (Czaczkes, Grüter, & Ratnieks, 2015; Grüter, Balbuena, & Farina, 2008). Unless stated otherwise, in this article we follow Shannon (1948) in defining information as something that reduces uncertainty about the state of the world. An information source is something that could potentially offer information, even if in a specific situation it may not. Thus, ‘memory’ is a private information source, but if there is nothing stored in the memory, it cannot provide information. Individuals can choose to use an information source by using its content to change their estimation of the state of the world (e.g. pay attention to a pheromone trail when attempting to locate a food source), but may choose not to.

While much research effort has been focused on assessing whether to exploit available information or innovate by gathering

* Correspondence: T. J. Czaczkes, Zoologie & Evolutionsbiologie, Universität Regensburg, Universitätsstr 31, Regensburg, 93053, Germany.

E-mail address: tomerczaczkes@ur.de (T. J. Czaczkes).

(often costly) new information (Danchin, Giraldeau, Valone, & Wagner, 2004; Laland, 2004), once information is gathered animals must decide how to use multiple information sources. Matters are complicated when conflicts arise between information sources. When this occurs, one option is to produce and follow a weighted intermediate value (von Thienen, Metzler, & Witte, 2016; Wehner, Hoinville, Cruse, & Cheng, 2016; Wystrach, Mangan, & Webb, 2015). For example, if one information source suggests a goal is northwest, and a second more preferred one suggests it is northeast, the animal might head north-northeast, as is seen, for example, in desert ants (Wystrach et al., 2015). However, sometimes an intermediate response is not possible, for example when deciding between two feeding locations. Alternatively, a hierarchy of information sources can be employed, with one type of information being exclusively used until it is not available, after which others begin to be employed; for example, honey bees use the sun's azimuth as a compass direction on cloudless days, but when the sun is not visible they rely on polarized light for this information (Dyer & Could, 1983; von Frisch, 1949). A more nuanced strategy is to weigh up the usefulness or information richness of different information sources, and follow the best one (Koops, 2004). It is possible that apparent hierarchical information use is in fact weighted intermediate use, with one option being overwhelmingly weighted above another.

Social insects, such as ants and bees, offer a unique system in which to study information use strategies (Grüter & Leadbeater, 2014; Leadbeater & Dawson, 2017). First, social information use is likely to be very well developed in this group. More fundamentally, however, in many aspects of information use by social insects, the interests of individuals are aligned within a colony. For example, we do not expect to see individuals from the same colony attempting to monopolize a resource. This should lead to full honesty in communication, making social signals more valuable, as there is no chance of deception, although information can still become outdated or resources overexploited (Beckers, Deneubourg, Goss, & Pasteels, 1990). Critically, it also means that information providers, rather than being exploited, are benefiting from providing information. This in turn is expected to result not only in strategic information use in the receiver, but also in strategic information provision by the signaller. The context in which social insects choose to actively produce social information can be as informative as the context in which they choose to respond to it (Grüter & Czaczkes, 2019; Grüter & Leadbeater, 2014). For example, ants that are more likely to make a mistake (and thus presumably are more uncertain) have been found to deposit less pheromone (Czaczkes & Heinze, 2015). Conversely, ants that initially make a wrong choice at a bifurcation when going to the food source, and then correct their mistake to eventually find the food source, deposit more pheromone than ants that initially make a correct decision (Czaczkes, Grüter, & Ratnieks, 2013; Czaczkes & Heinze, 2015). Ants from colonies in which individuals show poorer abilities to learn food locations tend to deposit more pheromone when returning from a food source (Pasquier & Grüter, 2016). There are also reports of ants depositing pheromone to lower-quality resources only in the dark (Cammaerts & Cammaerts, 1980).

These attributes should, in principle, strengthen the effect of social information on the behaviour of social insects. It is therefore surprising that in most cases in which conflict between social signals and private information have been studied, ants and bees predominantly follow their own memories (Almeida, Camargo, Forti, & Lopes, 2018; Aron, Beckers, Deneubourg, & Pasteels, 1993; Cosens & Toussaint, 1985; Fourcassie & Beugnon, 1988; Grüter, Czaczkes, & Ratnieks, 2011; Grüter et al., 2008; Harrison, Fewell, Stiller, & Breed, 1989; Quinet & Pasteels, 1996; Rosengren & Fortelius, 1986; Stroeymeyt, Franks, & Giurfa, 2011; Traniello,

1989). While this is not a universal pattern (Aron et al., 1993; Middleton, Reid, Mann, & Latty, 2018; Vilela, Jaffé, & Howse, 1987), it is nevertheless striking, as one might a priori expect social insects to prioritize social information.

One reason for ignoring social information is that it is often less informative than memories. For example, while the number and rate of waggle runs, and intensity of pheromone deposition, increase with resource quality, the inter- and intraindividual variation in describing resource quality is very large (Seeley, Mikheyev, & Pagano, 2000; Wendt, Strunk, Heinze, Roeder, & Czaczkes, 2019). By contrast, private memories of a food source's quality are very accurate, with *Lasius niger* being able to distinguish between, and reliably follow cues to, sucrose sources differing by just 0.1 M (De Agrò, Grimwade, & Czaczkes, 2019). It is possible that insects are attempting to follow a 'copy if better' strategy (Laland, 2004), but without accurate quality information rarely copy. Using a 'copy if better' strategy implies exploiting private information (memory) until social information reveals the presence of better options. Indeed, when unambiguous quality information about a better food source is provided, *L. niger* ants switch from following memories to following pheromone trails (Czaczkes, Beckwith, Horsch, Hartig, 2019). Reversals in information use, from reliance on memories (private information) to reliance on social signals (social information), allow us to understand the strategies animals use when choosing information sources.

Another important reversal in social information use was reported for *Formica pratensis* (Beugnon & Fourcassie, 1988; Fourcassie & Beugnon, 1988). During daylight hours and in a well-lit laboratory, these wood ants followed memories over pheromone trails. However, at night their behaviour reversed, and they preferentially followed pheromone trails. While these studies were purely descriptive, and did not involve experimental manipulation of light levels, they nevertheless suggested that ants may be following a 'copy when uncertain' strategy, only relying on chemical signals when memories are unavailable or unreliable. As visual information becomes scarcer one expects a heavier reliance on olfactory information, and indeed such a pattern is found in the brain anatomy of congeneric diurnal and nocturnal species of the Australian bull ant, *Myrmecia*: the former develop larger optic lobes and the latter larger olfactory neuropils (Sheehan, Kamhi, Seid, & Narendra, 2019). Copy when uncertain strategies have been reported in other social insects in other contexts, such as flower choice in bumblebees (Smolla, Alem, Chittka, & Shultz, 2016) and during nest relocation in rock ants (Stroeymeyt, Giurfa, & Franks, 2017).

The use and provision of information by animals under different light regimes offers a promising means of studying information conflict and information use strategies. Variation in light levels over many orders of magnitude is a challenge many animals must cope with every day–night cycle. This variation in light levels results in strong variation in the certainty of visual route memories, the main source of navigational information for many ants (Collett, Chittka, & Collett, 2013; Evison, Petchey, Beckerman, & Ratnieks, 2008; Graham & Cheng, 2009). Here, we studied the use and provision of social information (i.e. following and depositing pheromone trails) under different light levels in the ant *L. niger*. Under high light levels, *L. niger* preferentially follow private route memories over pheromone trails, even if the pheromone trails are very strong (Czaczkes et al., 2019; Grüter et al., 2011). We first confirmed that route memories in *L. niger* are based solely on visual cues at high light levels (as reported by Evison et al., 2008). We then asked whether *L. niger* foragers modulate their pheromone depositing (social information production) in response to different light levels. Finally, we assessed their preference for private information (memories) over social information (pheromone trails) at different light levels.

METHODS

Study Species

Colony fragments (henceforth 'colonies') of *L. niger* were collected from Falmer in East Sussex, U.K. Each colony was housed in a plastic container (30 × 30 cm and 10 cm high) with a plaster of Paris base containing a circular nest cavity constructed from plaster of Paris (13.5 cm diameter × 1.5 cm high) and covered by a disc of dark card. All colonies were queenless with 1000–3000 workers and small numbers of brood, each colony stemming from a different wild queenright colony. Queenless colonies readily forage, produce trails and are commonly used in behavioural experiments (Dussutour, Fourcassie, Helbing, & Deneubourg, 2004; Evison et al., 2008), remaining viable for 18 months or more. Colonies regulate the ratio of foragers and intranidal workers, ensuring a good mix of both. The ants were fed three times a week on a Bhatkar mix (Bhatkar & Whitcomb, 1970), with ad libitum access to water. Colonies were maintained at ambient laboratory light and temperature levels, and thus experienced a ca. 12:12 h light:dark cycle. Data were collected throughout the year. To ensure foraging motivation, feeding was stopped 4 days prior to experimentation.

General Experimental Design

Following the method of Grüter et al. (2011) we constructed a foraging trail as shown in Fig. 1. A white cardboard bridge (20 × 2 cm) connected the colony container to a transparent polycarbonate plastic T-maze covered with white paper. The stem of the T was 15 cm long and each branch was 11 cm long, with a consistent width of 2 cm. Experiment 1 was run in a small windowless room with an ambient temperature of 22 °C. Experiments 2 and 3 were carried out in a small room containing various items of laboratory equipment and furniture which served as visual landmarks for the foraging ants. We used three light levels in our experiments: bright light (3200 lx, emulating a cloudy but bright day), moderate light (10 lx, emulating dusk) and darkness (0.0007 lx, emulating a moonless night). Light intensity was measured repeatedly throughout the experiments using a photometer (LI-

COR inc; model LI-188B) to ensure illumination was consistent within treatment replicates. A portable halogen work light (IP 44; model NXS-500P) with a 500 W halogen bulb was used to provide high-intensity illumination for the bright-light treatment and a floor lamp with a 230 W linear halogen bulb and dimmer switch (Dar; model OPU 4946) provided illumination for the moderate light treatment. In the moderate light and darkness experiments, red light was used to provide illumination for experimental working and behavioural observations, but this long-wavelength illumination was not detectable by the ants; as in humans, most insects have trichromatic vision (UV, blue and green in the case of insects; Briscoe & Chittka, 2001; but see Yilmaz, Dyer, Rössler, & Spaethe, 2017 for evidence of bichromatic vision in an ant). However, their visible spectrum is shifted towards shorter wavelengths than ours (Menzel, 1979; Yilmaz et al., 2017); for example the spectral sensitivity maxima (λ_{\max}) for the ants *Atta sexdens* and *Camponotus blandor* are 500 nm and 570 nm, respectively (Martinoya, Bloch, Ventura, & Puglia, 1975; Yilmaz et al., 2017), and thus considerably shorter than the 700 nm found in humans (Autrum, 1968). To provide pure red light, a sleeve created from two-ply corrugated cardboard was tightly fitted over the hood of an angle poise lamp with a 60 W bulb. Two 50 mm square and 665 nm long pass filters (Schott; model FRG-66550) were slotted tightly together into a hole cut in the centre of the cardboard hood so that, when switched on, the lamp only provided red light.

Experiment 1: Does Light Level Affect Pheromone Depositing?

Ants were allowed to locate and feed on a drop of 1 M sucrose solution, randomly allocated to the end of the left or right branch of the T-maze (Fig. 1a). A 5 cm long section of paper, located just before the branches of the T, was marked by lines at either end, and a video camera (Sony; model HDR-XR520) was positioned to record, from the side, all pheromone-laying behaviour of ants walking along this designated section (Fig. 1a). This section was chosen because ants were observed to regularly deposit pheromone near the junction and for ease of monitoring. The low lux camera setting was used for the moderate light and darkness treatments. Owing to the lower video quality in this setting, it is

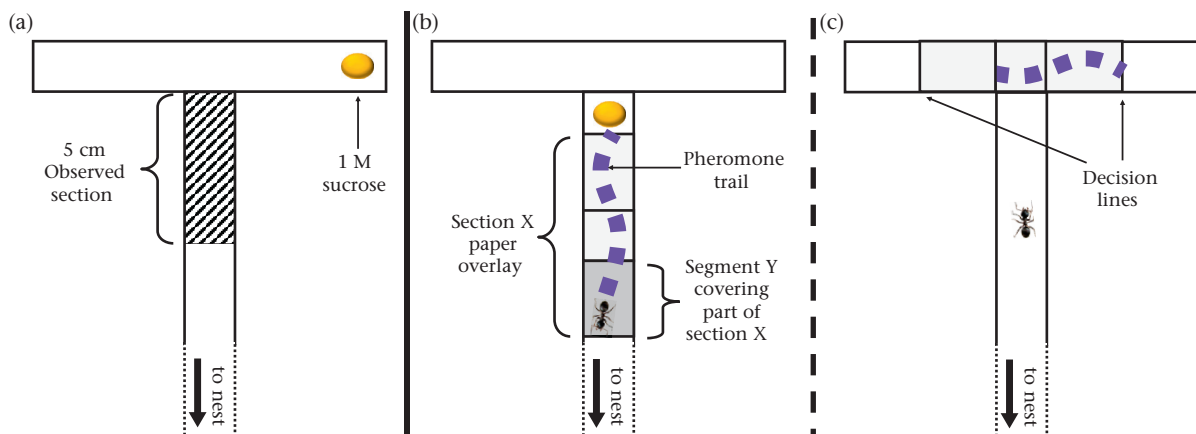


Figure 1. (a) Experimental design used to measure the frequency of depositing trail pheromone by foraging ants under three different light levels (darkness, moderate and bright). For each treatment, frequency of depositing was recorded for the observed section (lined area) for three journeys: the first return journey to the nest, the first outward journey to the food source and the second return to the nest. Each experiment involved 8–12 ants that were marked with paint while feeding on the sugar solution for the first time. (b) Experimental design used to acquire trail pheromone for subsequent conflict situations. A section of paper (X) was partially covered by a segment (Y) and ants were allowed to forage on a 1 M sugar solution. Pheromone deposits on the uncovered part of section X were monitored until 35–40 were reached, after which foraging was stopped and section X was transferred to a second T-maze for experiment 2. Segment Y was discarded, resulting in a pheromone-free part of section X. (c) Experimental design used for experiment 2. Ants were allowed to locate a 1 M sugar solution on a randomly chosen branch. While feeding, ants were marked with a paint dot and allowed to return to the nest. Section X was then transferred to the bifurcation so that marked returning ants were faced with a conflict between their route memory and trail pheromone. Decisions were recorded once an ant passed either of the two decision lines. Naïve ants with no memory were also tested to determine their response to pheromone alone, and as a control for any side bias.

possible that pheromone depositing in the moderate light and darkness treatments was underestimated. Depending on foraging activity of the colony, the first 8–12 ants that reached the food source and began to feed were marked with a dot of grey acrylic paint (the most discernible colour under infrared light). All unmarked ants were removed from the bridge and T-maze. Further access to the set-up was controlled by raising or lowering the bridge. The marked ants were allowed to find their way back to the nest, return to the food source and then once again return towards the nest. Only marked ants were allowed to re-enter the set-up by only lowering the bridge when marked ants were present. Unmarked ants that climbed the bridge were gently brushed off. We thus tested batches of 8–12 ants simultaneously. Marked ants were removed after passing through the observation section on this final trip. Thus, a maximum of three journeys were recorded for each ant: the first return to the nest, the first return to the food and the second return to the nest. When analysing the videos we assumed that an ant deposited a drop of pheromone each time we saw it clearly curve and dip its gaster to the surface (Beckers, Deneubourg, & Goss, 1992). The experiment was carried out under the three different lighting regimes using six colonies.

Experiment 2: Effect of Illumination on Information Use

To test whether reliance on trail pheromones increases at lower light levels, foraging ants were presented with a conflict between their own route memory and a pheromone trail at a T-junction at the three different light levels. Following Grüter et al. (2011), a pheromone trail was created by allowing ants to freely forage on a drop of 1 M sucrose situated on the T-maze before the bifurcation (Fig. 1b). A piece of paper (section X in Fig. 1b; 10×2 cm) was placed directly before the food source with a section of it (4×2 cm) covered by an additional piece of paper (segment Y). This ensured that the covered section beneath segment Y remained free from pheromone deposited by ants leaving and returning to the food source. A consistent pheromone trail strength was achieved by ending foraging once 35–40 pheromone deposits had been recorded. The maximum time allowed for trail establishment was 20 min; if the minimum number of deposits was not reached in this time, the experiment was terminated.

Ants were then given an opportunity to learn a food location by placing a 1 M sugar solution source on the end of a randomly selected branch of the T-maze and allowing the ants to find the food source via the bridge. Feeding ants were marked with a dot of grey acrylic paint and allowed to return to the nest. At high motivation levels such as these, 75–80% of *L. niger* foragers take the correct arm of an unmarked T-maze at normal levels of illumination after only one visit (Grüter et al., 2011; Oberhauser, Koch, & Czaczkes, 2018). Before these marked ants left the nest to find the food source again, section X was transferred to the bifurcation of the T-maze (Fig. 1c) with the pheromone-marked side placed on the branch opposite to where the food source had initially been situated. The covering segment Y was removed so that the bifurcation now had two new arms, only one of which was marked with pheromone. The decisions of the returning marked ants were then recorded. The maximum time allowed for memory development and subsequent decisions by the ants was 30 min, giving a total maximum experimental time of 50 min, when including trail establishment, which corresponds to the mean trail lifetime (time until pheromone depositing stops influencing behaviour) reported for *L. niger* (Beckers, Deneubourg, & Goss, 1993; Evison et al., 2008). Decisions were recorded for ants from nine colonies. One of the colonies was previously used in experiment 1. All colonies stemmed from different wild queenright colonies.

Experiment 3: Is Memory Based Solely upon Visual Cues?

The aim of this experiment was to investigate whether ants could develop a route memory in the absence of visual cues. As in experiment 2 the nest was connected to the T-maze by a cardboard bridge and a 1 M sucrose solution was placed at the end of a randomly assigned branch. In darkness (0.0007 lx), foraging ants were allowed to locate the food source and were subsequently marked with grey acrylic paint while feeding. Unmarked ants were removed from the maze and marked ants were allowed to return to the nest. Fresh paper was placed on the T-maze to remove any pheromone present and the binary choices made by returning marked ants at the T-junction were recorded. In addition, unmarked naïve ants were also allowed onto the maze, and their choices recorded. Ten colonies were used in this experiment, six of which were also used in experiment 2.

Statistical Analysis

Data for the pheromone-depositing frequency were found to be zero inflated so we chose to use the MCMCglmm package (Hadfield, 2010) implemented in R v. 2.14.2 (R Core Team, 2012) using the zipoisson family function. Uninformative prior distributions were used for fixed-effect parameters with a mean of 0 and a large variance of 10^8 . Priors for the variance components were inverse-Wishart distributed with the degree of belief parameter (n) set at $\frac{1}{4} \times 0.01$ and variance (V) limited to 1. Each model was run for 120 000 Markov chain Monte Carlo (MCMC) simulation iterations with a burn-in of 40 000 iterations and a thinning interval of 10 iterations. Autocorrelation between successive iterations was low (<0.05). Maximal models were created and nonsignificant fixed effects were sequentially removed from the model. Models were compared using the deviance information criterion (DIC). The fixed effects included light treatment (levels of bright, moderate and darkness) and journey (towards nest (1 and 2) and towards food source) while colony and date were used as independent random effects. Mean parameter estimates and 95% credible intervals (CI) were constructed and are reported in the Results; where estimates do not range over zero, the parameter is deemed to be significant.

Data from experiments 2 and 3 were analysed using generalized linear mixed-effect models (GLMM) with binomial errors in R v.3.4.1 (R Core Team, 2012). Models were fitted using the lmer function (Bates, Mächler, Bolker, & Walker, 2015). Following Forstmeier and Schielzeth (2011), models were constructed based on a priori expectations. Differences in choice behaviour for the null hypothesis were calculated using binomial tests. In experiment 3 the null hypothesis is 0.5 (random choice). In experiment 2, we compared the choice of the ants in the presence of pheromones (trained ants: information conflict) to the choice they would have made in the absence of pheromones (naïve ants: no information conflict). Data from experiment 3 provide a null hypothesis baseline for the behaviour of trained ants in darkness (0.46 do not follow their memory). The null hypothesis for bright light can be taken from Grüter et al. (2011) as 0.25. As no empirical data are available for providing a null hypothesis level for moderate light, we took an intermediate value between 0.46 and 0.25 as the null hypothesis: 0.36.

We found that naïve ants followed pheromone trails while trained ants in darkness did not, although the pairwise comparison between these groups was nonsignificant (see Results). However, the sample size for trained ants in darkness was much lower than for naïve ants (59 versus 147 ants). Thus, to test whether the difference in pheromone following found in these two groups was due to lower power in the dark-trained ant group, we ran a power analysis. To do this, we drew 1000 random subsamples of 59

individuals (the sample size of the dark-trained group) from the naïve group data and ran an identical binomial test on each subsample to that carried out on the dark-trained ants. We could then calculate the average number of times these smaller subsamples were significantly different from chance. This result was then corrected for multiple testing by subtracting the expected number of false positives.

Ethical Note

Lasius niger is not a threatened species and no licence is required for work with them. Only workers from mature colonies were collected, without destroying the mother colony. *Lasius niger* colonies easily withstand food deprivation of up to a week with no ill effects. Tested workers that could not be returned to the colony were rapidly killed by freezing to minimize distress.

RESULTS

Experiment 1: Does Light Level Affect Pheromone Depositing?

As light level dropped from bright to moderate, pheromone depositing increased significantly from 0.45 deposits per passage to 0.76 (parameter estimate = 1.477, 95% CI = 2.77, 0.122; near darkness versus bright; parameter estimate = 1.206, 95% CI = 2.27, 0.167; Fig. 2). However, pheromone depositing did not continue to increase when light levels were further reduced from 10 lx to 0.0007 lx [mean 0.73 deposits per passage, parameter estimate = -0.488, 95% CI = -1.78, 0.884]. Although pheromone depositing in the moderate and darkness treatments may be underestimated (see Methods), the fact that it nevertheless increased as light levels fell reinforces our results, indicating that the true pattern is even stronger than the one we report.

While the pattern of increasing pheromone depositing with decreasing light intensity held over all three visits, the specifics differed. Significantly more deposits were made on the first journey back to the nest under the moderate light level compared to the other two light treatments (moderate versus bright: 0.99 versus

0.39, parameter estimate = 2.18, 95% CI = 0.605, 3.71; moderate versus darkness: 0.99 versus 0.39, parameter estimate = 2.31, 95% CI = 1.05, 3.6; Fig. 3a). Of particular note is the significantly greater number of deposits on the return journey from the nest to the food source in darkness than in either moderate or bright light levels (darkness versus moderate: 0.81 versus 0.41, parameter estimate = 2.25, 95% CI = 3.51, 0.88; darkness versus bright: 0.81 versus 0.18, parameter estimate = 2.18, 95% CI = 3.97, 0.6; Fig. 3b). On the second return journey to the nest, pheromone depositing was almost one deposit per passage in both darkness and moderate light, but in each case this did not differ significantly from the 0.77 deposits per passage found in bright light conditions (darkness versus bright: 0.96 versus 0.77, parameter estimate = -0.462, 95% CI = -2.21, 1.16; moderate versus bright: 0.96 versus 0.77, parameter estimate = -0.834, 95% CI = -2.37, 0.884; Fig. 3c). There was no significant difference in the rate of pheromone depositing between the two return journeys to the nest in either the bright or moderate light conditions (bright: 0.39 versus 0.77, parameter estimate = 0.565, 95% CI = -0.842, 1.73; moderate: 0.99 versus 0.96, parameter estimate = -0.174, 95% CI = -1.35, 1.02), but in darkness pheromone depositing increased significantly on the second return journey (dark: 0.39 versus 0.96, parameter estimate = 1.07, 95% CI = 0.085, 1.93).

Experiment 2: Effect of Illumination on Information Use

The proportion of ant foragers following the pheromone trail rather than their route memories increased with decreasing light intensity (Fig. 4a). Under bright light only 28% of ants chose the pheromone-treated branch, significantly less than the 61% seen in darkness ($Z = -3.56$, $P < 0.001$). More ants followed the pheromone trail in darkness than in moderate light (44%; $Z = 1.9$, $P = 0.059$) and in moderate light versus bright light ($Z = 1.78$, $P = 0.076$), but these trends were not significant. Naïve ants followed the pheromone trail at the highest rate, which was significantly more than ants in bright and moderate light levels (versus bright: $Z = 5.51$, $P < 0.001$; versus moderate: $Z = 3.70$, $P < 0.001$), but not different to ants in darkness ($Z = 1.45$, $P = 0.15$). The random effect of colony contributed very little to the overall variance (<0.1%). Ants in the bright light treatment significantly preferred to follow their memories (exact binomial test with null hypothesis of 0.5: 16/59, $P < 0.001$), and their behaviour did not differ from that of ants in a nonconflict situation (binomial test, null hypothesis 0.25: $P = 0.76$). The decisions of ants under moderate light and darkness did not differ significantly from random (moderate light: 25/58, $P = 0.36$; darkness: 36/60, $P = 0.16$). However, for ants in darkness this represented an increased reliance on trail pheromones, as ants followed their memory significantly less often than ants in darkness in a nonconflict situation (null hypothesis 0.46: $P = 0.037$). Ants at moderate light levels behaved as predicted in a nonconflict situation (null hypothesis 0.35: $P = 0.22$). Naïve ants significantly preferred to follow the pheromone-marked path (106/148, $P < 0.001$).

We interpret these results as ants following a 'copy when uncertain' rule (see Discussion). These results rule out an otherwise plausible alternative explanation, which is that as light levels decrease ants make more errors. This is ruled out because the excess proportion of ants not following their memory was significantly above the null hypothesis rate in the darkness treatment (0.61–0.46 = 0.15) but not in the moderate light (0.44–0.35 = 0.09) and bright light (0.28–0.25 = 0.03) treatments. If error rates were driving the low memory following in the darkness treatment, we would expect the behaviour of ants to match the null hypothesis rate.

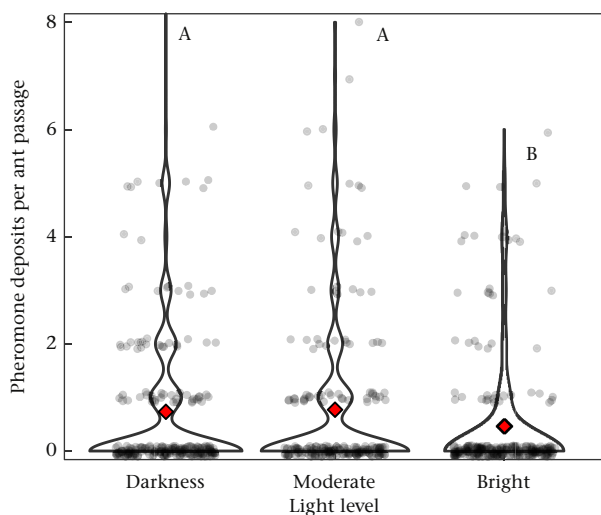


Figure 2. Violin plots show the number of pheromone deposits per passage for the three light levels (darkness, moderate and bright) for the three journeys combined. Circles are individual data points and red diamonds denote means. Different letters (A, B) signify significant ($P < 0.05$) differences between groups. The figure is cropped at eight deposits for clarity, omitting one data point in the 'dark' treatment. A slight jitter was added to allow individual points to be distinguished.

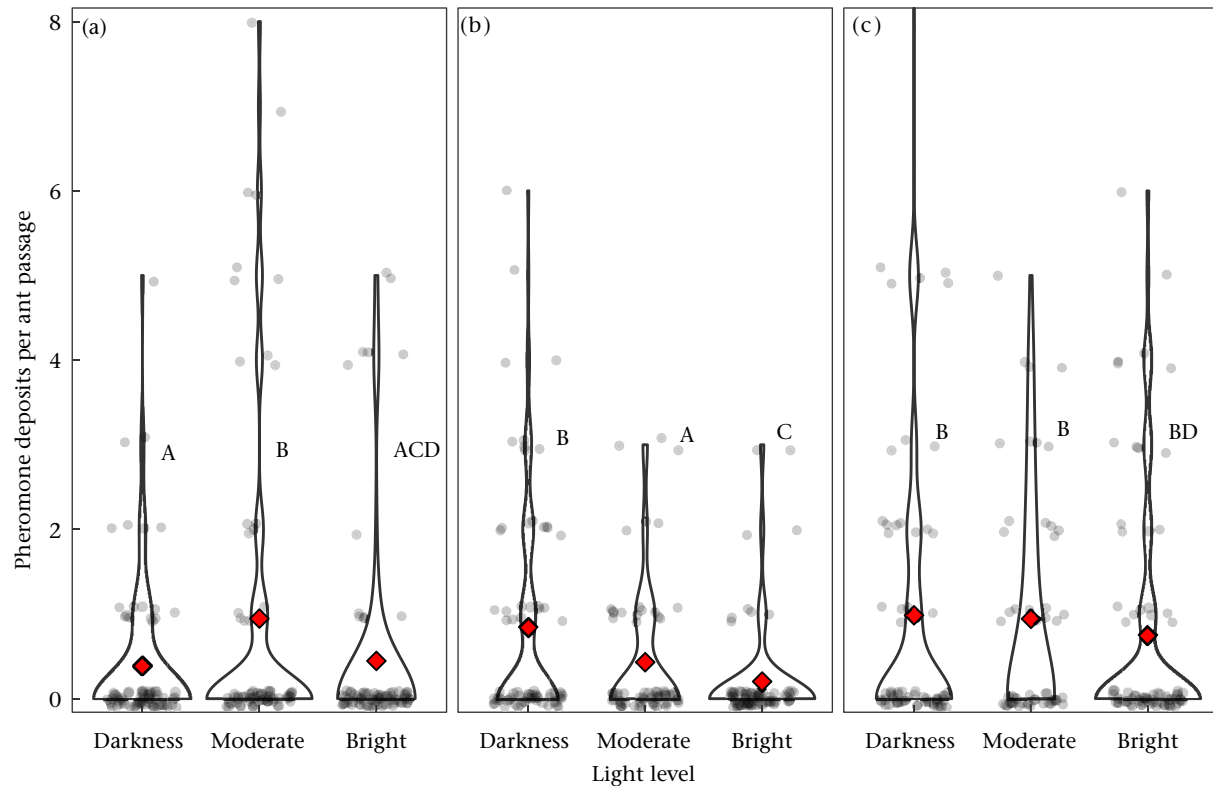


Figure 3. Violin plots show pheromone deposits per passage for each of the three light levels (darkness, moderate and bright) for the three separate journeys: (a) first return to nest, (b) outgoing to food and (c) second return to nest. Circles are individual data points and red diamonds denote means. Different letters (A,B,C,D) signify significant ($P < 0.05$) differences between groups. A slight jitter was added to allow individual points to be distinguished. Note that one data point in (c) in the darkness treatment was omitted for clarity, as in Fig. 2.

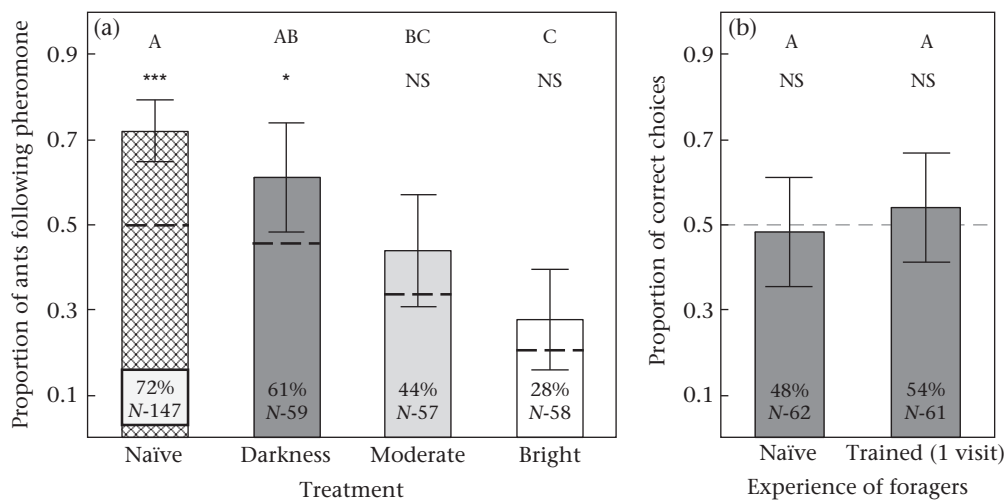


Figure 4. (a) Histogram showing the proportion of ants choosing the branch of a T-maze treated with trail pheromone when presented with a conflict between their own route memory (acquired from one visit) and trail pheromone, in the three light levels (darkness, moderate and bright). A comparison is also made to naïve ants with no route memory. (b) Histogram showing the proportion of ants choosing the branch of a T-maze that leads to a food source in darkness. Different letters (A,B,C, given above each bar) denote significant differences between groups, derived from post hoc analysis of GLMMs. Asterisks denote differences from the null hypothesis, derived from binomial tests: *** $P < 0.001$; * $P < 0.05$. Null hypothesis (dashed) lines represent the expected behaviour of the ants given no conflict: 0.5 for naïve ants and trained ants in (b), 0.46 for ants in darkness in (a) (the reciprocal of trained ants in (b)), 0.25 for ants in bright light (based on Grüter et al., 2011) and 0.35 for ants in moderate light (an intermediate value between 0.46 and 0.25). Error bars represent 95% confidence intervals. Percentages of ants following the pheromone trail (a) or choosing the arm where food was encountered (b) are shown in the bars together with the group sample size.

The pairwise comparison between naïve ants and darkness-trained ants given above indicated that pheromone following did not differ significantly between the two groups. However, our subsequent power analysis found that, when the sample size of the

naïve group was made identical to that of the darkness-trained group (59), the naïve ants' decisions were still significantly different from random 92.1% of the time. This implies that the difference between the naïve group and the dark-trained group,

although not found to be significant in the main model, is in fact real, with only a ca. 8% chance that it is not.

Experiment 3: Is Memory Based Solely upon Visual Cues?

Ants that had made one visit to a food source at the end of a T-maze under 0.0007 lx did not perform better than naïve ants when choosing a branch at the bifurcation (Fig. 4b). While 48% of naïve ants chose the branch to the food, only 54% of ants with a memory made the correct decision ($Z = 0.99$, $P = 0.31$). The random effect of colony and date contributed very little to the overall variance (<0.1%).

DISCUSSION

Light levels have a large effect on the way in which *L. niger* foragers make use of, and deposit, pheromone trails. As previously reported (Aron et al., 1993; Czaczkes et al., 2019; Grüter et al., 2011), when route memories (private information) and pheromone trails (social information) were in conflict in bright light (3200 lx), *L. niger* foragers mostly followed their route memories. However, we found that as light levels decreased to dusk-like levels (10 lx) and on to darkness (0.0007 lx), the rate at which ants relied on private information decreased. When in darkness ca. 60% of ants followed the pheromone trail, showing a significantly greater tendency to choose the nonmemory path (Fig. 4a) compared to ants not under information conflict (Fig. 4b). A shift in cue reliance due to light levels has been previously reported in field observations on *Formica polyctena* (Beugnon & Fourcassie, 1988) and *Formica nigricans* (Rosengren, 1977), but our study is the first to demonstrate this under stringently controlled laboratory conditions. This behaviour is consistent with ants following a 'copy when uncertain' strategy, in which reliance on social information increases as the quality of private information decreases. 'Copy when uncertain' is an adaptive information use strategy in many situations, and is employed by vertebrates in a variety of contexts (Galef, Dudley, & Whiskin, 2008; Jones, Ryan, Flores, & Page, 2013; Laland, 2004; van Bergen, Coolen, & Laland, 2004). Recently, behaviour consistent with 'copy when uncertain' has been described in *Temnothorax* rock ants during house hunting: informed ants rely more on social information about nest quality when their private information is uncertain (Stroeymeyt et al., 2017). Bumblebees in a foraging context have also been reported to 'copy when uncertain', being more likely to land next to bee models in uncertain environments (Smolla et al., 2016). Ants have also been reported to shift their reliance from visual to nonsocial odour cues in response to changes in light levels; when trained to locate food using both nonsocial scent cues (e.g. onion) and visual cues, various *Myrmica* species preferentially follow visual cues when olfactory and visual cues conflict. However, at lower light levels their preference shifts towards a reliance on olfactory cues, in some cases even when light levels are at a moderate level of 110 lx (Cammaerts, 2012; Cammaerts & Rachidi, 2009; Cammaerts, Rachidi, Beke, & Essaadi, 2012).

The rate of pheromone following in naïve ants in this study agrees well with previous data (Czaczkes, Castorena, Schürch, & Heinze, 2017; Grüter et al., 2011), but the pheromone-following rate of ants trained in darkness is lower and not different from chance. However, we were able to rule out the possibility that our results are driven by decreasing light levels increasing error rates, rather than increasing pheromone following. We are thus confident that our results reflect a real shift in information use. Note, however, that in this study ants were both trained and tested at the same light levels. This means that we cannot know the source of the reduction in private information quality. Ants may acquire less directional information in the dark, or they may be less able to use

it. It is also possible that ants can acquire and utilize directional information in the dark but choose not to use it. We consider this unlikely, however.

Our power analysis indicated that the difference in pheromone-following behaviour of naïve ants and darkness-trained ants is real. The lower pheromone-following rates of darkness trained-ants are likely to be driven by remaining conflict with memories. An alternative explanation is that the ants were in a 'wrong-task state' (Czaczkes et al., 2017; Roces, 1993); naïve ants might have been actively scouting (exploring or otherwise ready to make use of social information), while experienced ants might have been foraging, attempting to exploit private information even if it was not there, and disregarding social information. However, Czaczkes et al. (2017) showed that task state does not influence pheromone following. As both naïve ants and ants in a different task state but with no directional information did follow pheromone, we can be confident that the trained ants in darkness had access to the trail pheromone information.

Ants seem to learn very poorly in darkness, or not at all (54% correct choices), while they are very capable of doing so on almost identical mazes in lit conditions (ca. 75% correct choices; Grüter et al., 2011; Oberhauser et al., 2018). It is possible that, given more visits, ants would learn to navigate the maze reliably using idiothetic (internal body movement) cues, as has been shown in other ant species (Macquart, Latil, & Beugnon, 2008). Note that visual cues are in principle not required for navigation by path integration (Collett & Collett, 2000), where an odometer linked to any directional cue can be used to estimate displacement from a starting location. Magnetic cues have been shown to be used for navigation by several animals, including ants, especially when other cues are unavailable (Banks & Srygley, 2003; Lohmann, Lohmann, & Putman, 2007). Path integration is usually used as the initial navigation mechanism by desert ants, before route-based navigation memories are formed (Collett et al., 2013). If the same is true for *L. niger*, this would imply that *L. niger* require visual directional cues to perform path integration effectively.

Pheromone depositing in *L. niger* is very variable between workers, with most ants depositing nothing, and some making many deposits per passage. However, as pheromone deposits accumulate, it is the mean pheromone-depositing rates that are relevant to the colony. Inspection of these showed that rates of pheromone depositing varied strongly with light levels. Broadly, over all visits, ants deposited about 40% less pheromone in bright light than in the moderate light level or darkness (Fig. 2). Along with the poor navigational performance of ants in darkness, this supports the assertion that foragers are less confident of their location in moderate light levels and darkness. Previous studies have demonstrated that pheromone-depositing rates correlate with navigational confidence. For example, Czaczkes and Heinze (2015) trained ants to make return visits to a food source at the end of a T-maze, as in the current experiment. They found that pheromone-depositing rates of outgoing ants that would go on to make a navigational error were lower than those of ants that would make a correct decision. This implies that the ants had some measure of their own uncertainty or were vacillating between an informed and a naïve state. Once such 'mistaken' ants finally find the food source, they increase their pheromone-depositing rates on their return journey to the nest (Czaczkes et al., 2013; Czaczkes & Heinze, 2015; Czaczkes, Weichselgartner, Bernadou, & Heinze, 2016), presumably in an effort to provide more information on difficult-to-navigate routes. We suggest that the similar increase in pheromone depositing in dim light and darkness we report here is also best understood as an effort to increase information availability under challenging navigation conditions. Note, however, that in our experiment all ants were tested during their circadian

day. It is possible that pheromone depositing in darkness when ants 'expect' it to be dark may differ from what is reported here.

A more complex picture emerges when we examine each journey of the ants separately. On the first return to the nest, ants in moderate light deposited about 45% more pheromone than ants in darkness, and 20% more than ants in bright light (Fig. 3). We interpret this again in terms of certainty and information provisioning (Czaczkes et al., 2013; Czaczkes & Heinze, 2015). Thus, ants in moderate light can be interpreted as sensing that more information is needed compared to ants in bright light, and therefore provide this information. Ants in darkness deposited very little pheromone, but this is not surprising: ants that are lost or unexpectedly leave a pheromone trail deposit little or no pheromone (Czaczkes, Grüter, Jones, & Ratnieks, 2011; T. J. Czaczkes, personal observation). Surprisingly, on their return to the food source, outgoing ants in darkness on average deposited almost 78% more pheromone than ants returning in bright light. This was unexpected, given that they apparently could not know exactly where they were going (Fig. 4b). However, as some pheromone and home range markings had already been deposited, this might have acted as a reassurance that ants were on the right path (Czaczkes et al., 2011; Devigne, Renon, & Detrain, 2004; Wüst & Menzel, 2017). Given that they were on the right path, reinforcing the pheromone signal provided more information in darkness, where visual information was lacking. Finally, on the second return to the nest, ants consistently deposited a high amount of pheromone at all light levels. We interpret this as all ants, having found food twice in quick succession, were confident enough of their location to recruit strongly to the food source.

How animals strategically use and deploy information has been the subject of intense research (Dall et al., 2005; Grüter & Leadbeater, 2014; Laland, 2004). The information richness of an information source is predicted to be a strong driver of its use (von Thienen et al., 2016). Studying visual information use under varying light levels provides a powerful and ecologically relevant means of manipulating information richness. By taking advantage of this, we have shown that information use during *L. niger* foraging is consistent with a 'copy when uncertain' strategy. We have also demonstrated that ants vary their provision of an alternative information source as their primary information source becomes less informative.

Author Contributions

S.J. and J.B. conceived of the study. S.J. planned the study. S.J. and T.J.C. performed the statistical analysis. F.B.O. performed the power analysis. S.J., A.G. and E.G. collected the data. T.J.C., S.J. and J.B. wrote the manuscript. All authors gave final approval for this work.

Acknowledgments

Thanks to Stephanie Wendt for help with the violin plots and to Nathalie Stroeymeyt and an anonymous referee for their very valuable comments on the manuscript. S.J. was funded by the British Biotechnology Research Council (BBSRC). T.J.C. was funded by a Deutsche Forschungsgemeinschaft Emmy Noether grant number CZ 237/1-1.

References

Almeida, N. G. D., Camargo, R. D. S., Forti, L. C., & Lopes, J. F. S. (2018). Hierarchical establishment of information sources during foraging decision-making process involving *Acromyrmex subterraneus* (Forel, 1893) (Hymenoptera, Formicidae). *Revista Brasileira de Entomologia*. <https://doi.org/10.1016/j.rbe.2017.11.006>.

- Aron, S., Beckers, R., Deneubourg, J., & Pasteels, J. M. (1993). Memory and chemical communication the orientation of two mass-recruiting ant species. *Insectes Sociaux*, 40(4), 369–380. <https://doi.org/10.1007/BF01253900>.
- Autrum, H. (1968). Colour vision in man and animals. *Naturwissenschaften*, 55(1), 10–18.
- Banks, A. N., & Srygley, R. B. (2003). Orientation by magnetic field in leaf-cutter ants, *Atta colombica* (Hymenoptera: Formicidae). *Ethology*, 109(10), 835–846. <https://doi.org/10.1046/j.0179-1613.2003.00927.x>.
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1). <https://doi.org/10.18637/jss.v067.i01>.
- Beckers, R., Deneubourg, J., & Goss, S. (1992). Trail laying behaviour during food recruitment in the ant *Lasius niger* (L.). *Insectes Sociaux*, 39, 59–71.
- Beckers, R., Deneubourg, J. L., & Goss, S. (1993). Modulation of trail laying in the ant *Lasius niger* (Hymenoptera: Formicidae) and its role in the collective selection of a food source. *Journal of Insect Behavior*, 6(6), 751–759. <https://doi.org/10.1007/BF01201674>.
- Beckers, R., Deneubourg, J. L., Goss, S., & Pasteels, J. M. (1990). Collective decision making through food recruitment. *Insectes Sociaux*, 37(3), 258–267.
- van Bergen, Y., Coolen, I., & Laland, K. N. (2004). Nine-spined sticklebacks exploit the most reliable source when public and private information conflict. *Proceedings of the Royal Society B: Biological Sciences*, 271(1542), 957.
- Beugnon, G., & Fourcassie, V. (1988). How do red wood ants orient during diurnal and nocturnal foraging in a three dimensional system? II. Field experiments. *Insectes Sociaux*, 35(1), 106–124. <https://doi.org/10.1007/BF02224142>.
- Bhatkar, A., & Whitcomb, W. H. (1970). Artificial diet for rearing various species of ants. *Florida Entomologist*, 53(4), 229–232.
- Briscoe, A. D., & Chittka, L. (2001). The evolution of color vision in insects. *Annual Review of Entomology*, 46(1), 471–510. <https://doi.org/10.1146/annurev.ento.46.1.471>.
- Cammaerts Tricot, M.-C. (2012). Navigation system of the ant *Myrmica rubra* (hymenoptera: Formicidae). *Myrmecological News*, 16, 111–121.
- Cammaerts Tricot, M.-C., Rachidi, Z., Beke, S. S., & Essaadi, Y. Y. (2012). Use of olfactory and visual cues for orientation by the ant *Myrmica ruginodis* (Hymenoptera: Formicidae). *Myrmecological News*, 16, 45–55.
- Cammaerts, M.-C., & Cammaerts, R. (1980). Food recruitment strategies of the ants *Myrmica sabuleti* and *Myrmica ruginodis*. *Behavioural Processes*, 5(3), 251–270. [https://doi.org/10.1016/0376-6357\(80\)90006-6](https://doi.org/10.1016/0376-6357(80)90006-6).
- Cammaerts, M.-C., & Rachidi, Z. (2009). Olfactive conditioning and use of visual and odorous elements for movement in the ant *Myrmica sabuleti* (Hymenoptera, Formicidae). *Myrmecology News*, 12, 117–127.
- Collett, M., Chittka, L., & Collett, T. S. (2013). Spatial memory in insect navigation. *Current Biology*, 23(17), R789–R800. <https://doi.org/10.1016/j.cub.2013.07.020>.
- Collett, M., & Collett, T. S. (2000). How do insects use path integration for their navigation? *Biological Cybernetics*, 83(3), 245–259. <https://doi.org/10.1007/s004220000168>.
- Cosens, D., & Toussaint, N. (1985). An experimental study of the foraging strategy of the wood ant *Formica aquilonia*. *Animal Behaviour*, 33(2), 541–552. [https://doi.org/10.1016/S0003-3472\(85\)80077-4](https://doi.org/10.1016/S0003-3472(85)80077-4).
- Czaczkes, T. J., Beckwith, J. J., Horsch, A.-L., & Hartig, F. (2019). The multi-dimensional nature of information drives prioritization of private over social information in ants. *Proceedings of the Royal Society Biological Sciences*, 20191136. <https://doi.org/10.1098/rspb.2019.1136>.
- Czaczkes, T. J., Castorena, M., Schürch, R., & Heinze, J. (2017). Pheromone trail following in the ant *Lasius niger*: High accuracy and variability but no effect of task state. *Physiological Entomology*, 42(1), 91–97. <https://doi.org/10.1111/phen.12174>.
- Czaczkes, T. J., Grüter, C., Jones, S. M., & Ratnieks, F. L. W. (2011). Synergy between social and private information increases foraging efficiency in ants. *Biology Letters*, 7(4), 521–524. <https://doi.org/10.1098/rsbl.2011.0067>.
- Czaczkes, T. J., Grüter, C., & Ratnieks, F. L. W. (2013). Ant foraging on complex trails: Route learning and the role of trail pheromones in *Lasius niger*. *Journal of Experimental Biology*, 216, 188–197. <https://doi.org/10.1242/jeb.076570>.
- Czaczkes, T. J., Grüter, C., & Ratnieks, F. L. W. (2015). Trail pheromones: An integrative view of their role in colony organisation. *Annual Review of Entomology*, 60, 581–599. <https://doi.org/10.1146/annurev-ento-010814-020627>.
- Czaczkes, T. J., & Heinze, J. (2015). Ants adjust their pheromone deposition to a changing environment and their probability of making errors. *Proceedings of the Royal Society B: Biological Sciences*, 282(1810), 20150679. <https://doi.org/10.1098/rspb.2015.0679>.
- Czaczkes, T. J., Weichselgartner, T., Bernadou, A., & Heinze, J. (2016). The effect of trail pheromone and path confinement on learning of complex routes in the ant *Lasius niger*. *PLoS One*, 11(3), e0149720. <https://doi.org/10.1371/journal.pone.0149720>.
- Dall, S. R. X., Giraldeau, L.-A., Olsson, O., McNamara, J. M., & Stephens, D. W. (2005). Information and its use by animals in evolutionary ecology. *Trends in Ecology & Evolution*, 20(4), 187–193. <https://doi.org/10.1016/j.jtree.2005.01.010>.
- Danchin, E., Giraldeau, L. A., Valone, T. J., & Wagner, R. H. (2004). Public information: From nosy neighbors to cultural evolution. *Science*, 305(5683), 487.
- De Agrò, M., Grimm, D., & Czaczkes, T. J. (2019). Irrational risk aversion in ants is driven by perceptual mechanisms. *BioRxiv*, 620054. <https://doi.org/10.1101/620054>.
- Devigne, C., Renon, A., & Detrain, C. (2004). Out of sight but not out of mind: Modulation of recruitment according to home range marking in ants.

- Animal Behaviour, 67(6), 1023–1029. <https://doi.org/10.1016/j.anbehav.2003.09.012>.
- Dussutour, A., Fourcassie, V., Helbing, D., & Deneubourg, J.-L. (2004). Optimal traffic organization in ants under crowded conditions. *Nature*, 428(6978), 70–73. <https://doi.org/10.1038/nature02345>.
- Dyer, F. C., & Could, J. L. (1983). Honey Bee Navigation: The honey bee's ability to find its way depends on a hierarchy of sophisticated orientation mechanisms. *American Scientist*, 71(6), 587–597.
- Evison, S. E. F., Petchey, O. L., Beckerman, A. P., & Ratnieks, F. L. W. (2008). Combined use of pheromone trails and visual landmarks by the common garden ant *Lasius niger*. *Behavioral Ecology and Sociobiology*, 63, 261–267. <https://doi.org/10.1007/s00265-008-0657-6>.
- Forstmeier, W., & Schielzeth, H. (2011). Cryptic multiple hypotheses testing in linear models: Overestimated effect sizes and the winner's curse. *Behavioral Ecology and Sociobiology*, 65(1), 47–55. <https://doi.org/10.1007/s00265-010-1038-5>.
- Fourcassie, V., & Beugnon, G. (1988). How do red wood ants orient when foraging in a three dimensional system? I. Laboratory experiments. *Insectes Sociaux*, 35(1), 92–105. <https://doi.org/10.1007/BF02224141>.
- von Frisch, K. (1949). Die Polarisation des Himmelslichtes als orientierender Faktor bei den Tänzen der Bienen. *Experientia*, 5(4), 142–148.
- Galef, B. G., Jr., Dudley, K. E., & Whiskin, E. E. (2008). Social learning of food preferences in 'dissatisfied' and 'uncertain' Norway rats. *Animal Behaviour*, 75(2), 631–637. <https://doi.org/10.1016/j.anbehav.2007.06.024>.
- Graham, P., & Cheng, K. (2009). Ants use the panoramic skyline as a visual cue during navigation. *Current Biology*, 19(20), R935–R937. <https://doi.org/10.1016/j.cub.2009.08.015>.
- Grüter, C., Balbuena, M. S., & Farina, W. M. (2008). Informational conflicts created by the waggle dance. *Proceedings of the Royal Society B: Biological Sciences*, 275(1640), 1321–1327. <https://doi.org/10.1098/rspb.2008.0186>.
- Grüter, C., & Czaczkes, T. J. (2019). Communication in social insects and how it is shaped by individual experience. *Animal Behaviour*, 151, 207–215. <https://doi.org/10.1016/j.anbehav.2019.01.027>.
- Grüter, C., Czaczkes, T. J., & Ratnieks, F. L. W. (2011). Decision making in ant foragers (*Lasius niger*) facing conflicting private and social information. *Behavioral Ecology and Sociobiology*, 64, 141–148. <https://doi.org/10.1007/s00265-010-1020-2>.
- Grüter, C., & Leadbeater, E. (2014). Insights from insects about adaptive social information use. *Trends in Ecology & Evolution*, 29(3), 177–184.
- Hadfield, J. D. (2010). MCMC methods for multi-response generalized linear mixed models: The MCMCglmm R package. *Journal of Statistical Software*, 33(2), 1–22.
- Harrison, J. F., Fewell, J. H., Stiller, T. M., & Breed, M. D. (1989). Effects of experience on use of orientation cues in the giant tropical ant. *Animal Behaviour*, 37(5), 869–871. [https://doi.org/10.1016/0003-3472\(89\)90076-6](https://doi.org/10.1016/0003-3472(89)90076-6).
- Heyes, C. M. (1994). Social learning in animals: Categories and mechanisms. *Biological Reviews*, 69(2), 207–231. <https://doi.org/10.1111/j.1469-185X.1994.tb01506.x>.
- Jones, P. L., Ryan, M. J., Flores, V., & Page, R. A. (2013). When to approach novel prey cues? Social learning strategies in frog-eating bats. *Proceedings of the Royal Society of London B Biological Sciences*, 280(1772), 20132330. <https://doi.org/10.1098/rspb.2013.2330>.
- Koops, M. A. (2004). Reliability and the value of information. *Animal Behaviour*, 67(1), 103–111. <https://doi.org/10.1016/j.anbehav.2003.02.008>.
- Laland, K. N. (2004). Social learning strategies. *Learning & Behavior*, 32(1), 4–14. <https://doi.org/10.1016/j.lbeh.2003.02.008>.
- Leadbeater, E., & Dawson, E. H. (2017). A social insect perspective on the evolution of social learning mechanisms. *Proceedings of the National Academy of Sciences*, 114(30), 7838–7845. <https://doi.org/10.1073/pnas.1620744114>.
- Lohmann, K. J., Lohmann, C. M. F., & Putman, N. F. (2007). Magnetic maps in animals: nature's GPS. *Journal of Experimental Biology*, 210(21), 3697–3705. <https://doi.org/10.1242/jeb.001313>.
- Macquart, D., Latil, G., & Beugnon, G. (2008). Sensorimotor sequence learning in the ant *Gigantiops destructor*. *Animal Behaviour*, 75(5), 1693–1701. <https://doi.org/10.1016/j.anbehav.2007.10.023>.
- Martinoya, C., Bloch, S., Ventura, D. F., & Puglia, N. M. (1975). Spectral efficiency as measured by ERG in the ant (*Atta sexdens rubropilosa*). *Journal of Comparative Physiology*, 104(2), 205–210. <https://doi.org/10.1007/BF01379460>.
- Menzel, R. (1979). Spectral sensitivity and color vision in invertebrates. In H. Autrum, M. F. Bennett, B. Diehn, K. Hamdorf, M. Heisenberg, M. Järvilehto, et al. (Eds.), *Comparative Physiology and Evolution of Vision in Invertebrates: A: Invertebrate Photoreceptors* (pp. 503–580). Berlin, Germany: Springer-Verlag. https://doi.org/10.1007/978-3-642-66999-6_9.
- Middleton, E. J. T., Reid, C. R., Mann, R. P., & Latty, T. (2018). Social and private information influence the decision making of Australian meat ants (*Iridomyrmex purpureus*). *Insectes Sociaux*, 65(4), 649–656. <https://doi.org/10.1007/s00040-018-0656-1>.
- Oberhauser, F. B., Koch, A., & Czaczkes, T. J. (2018). Small differences in learning speed for different food qualities can drive efficient collective foraging in ant colonies. *Behavioral Ecology and Sociobiology*, 72(10), 164. <https://doi.org/10.1007/s00265-018-2583-6>.
- Pasquier, G., & Grüter, C. (2016). Individual learning performance and exploratory activity are linked to colony foraging success in a mass-recruiting ant. *Behavioral Ecology*, 27(6), 1702–1709. <https://doi.org/10.1093/beheco/arw079>.
- Quinet, Y., & Pasteels, J. M. (1996). Spatial specialization of the foragers and foraging strategy in *Lasius fuliginosus* (Latreille) (Hymenoptera, Formicidae). *Insectes Sociaux*, 43(4), 333–346. <https://doi.org/10.1007/BF01258407>.
- R Core Team. (2012). *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from <http://www.R-project.org>.
- Roces, F. (1993). Both evaluation of resource quality and speed of recruited leaf-cutting ants (*Acromyrmex lundii*) depend on their motivational state. *Behavioral Ecology and Sociobiology*, 33(3), 183–189. <https://doi.org/10.1007/BF00216599>.
- Rosengren, R. (1977). Foraging strategy of wood ants (*Formica rufa* group). II. Nocturnal orientation and diel periodicity. *Acta Zoologica Fennica*, 150, 3–29.
- Rosengren, R., & Fortelius, W. (1986). Ortstreue in foraging ants of the *Formica rufa* group — hierarchy of orienting cues and long-term memory. *Insectes Sociaux*, 33(3), 306–337. <https://doi.org/10.1007/BF02224248>.
- Seeley, T. D., Mikheyev, A. S., & Pagano, G. J. (2000). Dancing bees tune both duration and rate of waggle-run production in relation to nectar-source profitability. *Journal of Comparative Physiology*, 186(9), 813–819. <https://doi.org/10.1007/s003590000134>.
- Shannon, C. E. (1948). A mathematical theory of communication. *Bell System Technical Journal*, 27(3), 379–423.
- Sheehan, Z. B. V., Kamhi, J. F., Seid, M. A., & Narendra, A. (2019). Differential investment in brain regions for a diurnal and nocturnal lifestyle in Australian *Myrmecia* ants. *Journal of Comparative Neurology*, 1–17. <https://doi.org/10.1002/cne.24617>.
- Smolla, M., Alem, S., Chittka, L., & Shultz, S. (2016). Copy-when-uncertain: Bumblebees rely on social information when rewards are highly variable. *Biology Letters*, 12(6), 20160188. <https://doi.org/10.1098/rsbl.2016.0188>.
- Stroeymeyt, N., Franks, N. R., & Giurfa, M. (2011). Knowledgeable individuals lead collective decisions in ants. *Journal of Experimental Biology*, 214(18), 3046–3054. <https://doi.org/10.1242/jeb.059188>.
- Stroeymeyt, N., Giurfa, M., & Franks, N. R. (2017). Information certainty determines social and private information use in ants. *Scientific Reports*, 7. <https://doi.org/10.1038/srep43607>.
- von Thienen, W., Metzler, D., & Witte, V. (2016). How memory and motivation modulate the responses to trail pheromones in three ant species. *Behavioral Ecology and Sociobiology*, 70(3), 393–407. <https://doi.org/10.1007/s00265-016-2059-5>.
- Traniello, J. F. A. (1989). Chemical trail systems, orientation, and territorial interactions in the ant *Lasius neoniger*. *Journal of Insect Behavior*, 2(3), 339–354. <https://doi.org/10.1007/BF01068060>.
- Vilela, E. F., Jaffé, K., & Howse, P. E. (1987). Orientation in leaf-cutting ants (formicidae: Attini). *Animal Behaviour*, 35(5), 1443–1453. [https://doi.org/10.1016/S0003-3472\(87\)80017-9](https://doi.org/10.1016/S0003-3472(87)80017-9).
- Wehrer, R., Hoinville, T., Cruse, H., & Cheng, K. (2016). Steering intermediate courses: desert ants combine information from various navigational routines. *Journal of Comparative Physiology*, 202(7), 459–472. <https://doi.org/10.1007/s00359-016-1094-z>.
- Wendt, S., Strunk, K. S., Heinze, J., Roeder, A., & Czaczkes, T. J. (2019). Relative value perception in an insect: Positive and negative incentive contrasts in ants. *eLife*. <https://doi.org/10.7554/eLife.45450>.
- Worden, B. D., & Papaj, D. R. (2005). Flower choice copying in bumblebees. *Biology Letters*, 1(4), 504–507. <https://doi.org/10.1098/rsbl.2005.0368>.
- Wüst, M., & Menzel, F. (2017). I smell where you walked — how chemical cues influence movement decisions in ants. *Oikos*, 126(1), 149–160. <https://doi.org/10.1111/oik.03332>.
- Wystrach, A., Mangan, M., & Webb, B. (2015). Optimal cue integration in ants. *Proc. R. Soc. B*, 282(1816), 20151484. <https://doi.org/10.1098/rspb.2015.1484>.
- Yilmaz, A., Dyer, A. G., Rössler, W., & Spaethe, J. (2017). Innate colour preference, individual learning and memory retention in the ant *Camponotus blandus*. *Journal of Experimental Biology*, 220(18), 3315–3326. <https://doi.org/10.1242/jeb.158501>.