ODOR SOURCE LOCATION CAN BE PREDICTED FROM A TIME-HISTORY OF ODOR STATISTICS FOR A LARGE-SCALE OUTDOOR PLUME

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ABSTRACT

Odor plumes in turbulent environments are intermittent and sparse, yet many animals effectively navigate to odor sources to find food [1]. Computational and lab-scaled experiments [2, 3, 4] have suggested that information about the source distance may be encoded in odor signal statistics, yet it is unclear whether useful and continuous distance estimates can be made under real-world flow conditions. Here we analyze odor signals from outdoor experiments with a sensor moving across large spatial scales in desert and forest environments to show that odor signal statistics can yield useful estimates of distance. The probability distribution of statistics from individual whiffs (contiguous odor sequences) are correlated with distance, but their correlation coefficient is poor. However, we show that a useful estimate of distance can be found by incorporating whiff statistics from time history of $\sim$10-seconds, resulting in a strong correlation of $\boldsymbol{R^2 \sim 0.70}$. We identified whiff concentration and duration to be the most informative features. By combining distance estimates from a linear model with wind-relative motion dynamics, we were able to estimate source distance in a 60x60 m^2 area with median errors of 3-8 meters, a distance at which point odor sources are within visual range for animals such as mosquitoes [5, 6]. Finally, we show that such estimates are only feasible if odor signal information is recorded at temporal resolutions of $\geq$20 Hz. Together, our results provide a compelling case for how odor signal statistics could be used by animals, or man-made machines, to optimize plume tracking decisions at large spatial scales with natural wind.

Keywords Odor plume statistics · olfactory navigation · chemical ecology

1 Introduction

Odor plumes serve as a crucial sensory signal for many organisms searching for food and mates [1], as well as robotic systems geared towards chemical leak detection [7, 8]. In outdoor environments, these plumes are transported by turbulent air currents, which break them into complex, intermittent, and time-varying patterns [9, 10, 11, 2]. As a result, a single encounter with an odor plume does not provide direct information about where the source is located. Despite the challenges imposed by this structure, a variety of organisms, including insects [12, 13, 14], crustaceans [15], fish [16], and mammals [17], excel at following turbulent odor plumes toward their source. Many of these animals are exquisitely sensitive to the precise timing [18], spatial structure [19], and history of odor encounters [20]. Both timing and statistics of the olfactory experience have been shown to drive behavioral decisions [4, 21, 22, 23, 24]. However, precisely what information can practically be extracted from the statistics of these olfactory signals over large spatial scales is an open area of investigation.

Insects, in particular, have served as fruitful models for studying long-range plume tracking behaviors, with moths and fruit flies tracking airborne plumes over 100 meters or more [25, 26]. However, in wind tunnel experiments they are

also attracted to visual features after encountering an odor [27, 12], which may be a general behavior to help in the final stages of source localization [5]. If insects were to approach every visual feature they encountered along a long-range plume tracking trajectory, they would never make it to the source. This paradox led us to ask the question: is it possible to recover accurate distance information from odor encounter statistics over large spatial scales? If so, it is possible that animals and machines alike could use this information to gate attraction to visual features, or modulate other aspects of their localization algorithms.

To describe the statistics of intermittent odor plumes we use the established term *whiff* to indicate a collection of odor encounters above some threshold (also referred to as *bouts*), and the term *blank* for anything below that threshold [2, 28]. Prior experiments suggest that both the intensity of whiffs (i.e. concentration) and their timing (e.g. whiff frequency) are correlated with distance. Celani et. al [2] showed agreement between theory and both lab and field experiments (from [29]) that the probability distributions of whiff frequencies and concentrations vary with distance for a stationary sensor. The ability to distinguish between these probability distributions using whiff data from a finite amount of time, and thus estimate distance in real-time, especially in the field where wind can be quite variable in both speed and direction [30], is unclear. Additional experiments on spatial scales of a meter or so using experimental and computational approaches and stationary sensors have further confirmed that both timing and intensity of odor whiffs carry information correlated with distance to the source [28, 31, 32, 3]. Additionally, the variance of whiff frequency appears to be correlated with position perpendicular to the plume centerline in a wind tunnel [3]. Across these studies researchers have used a diversity of statistics to characterize whiff structure, including: mean odor concentration, whiff frequency, average slope of whiffs, average duration of blanks and whiffs, intermittency factor, and variance of whiff frequency. Do insects modulate behavior according to these statistics? Experiments with walking flies [4] have shown that at least one of these features–whiff frequency–does play an important role in flies' decisions to turn upwind. Whether odor statistics such as whiff intensity and frequency provide meaningful distance information over the large spatial scales over which natural plume tracking behaviors occur for flying insects, however, remains an open question.

In this paper, we tested whether the timing and concentration features of an odor signal are correlated with distance from the source in outdoor environments at spatial scales of 60x60 m^2. We found that features of individual whiffs have a very weak correlation with distance from the source. However, by accumulating odor signal statistics–specifically whiff concentration and duration–over a 10-second time window it is possible to estimate the distance to an odor source with surprising accuracy, especially under consistent wind conditions.

Results

Outdoor measurements of odor plumes

To investigate the correlation between odor signal statistics and distance to the source, we collected data in two environments. First, we selected a flat desert playa in Northern Nevada's Black Rock Desert (Fig. 1A). We used a propylene tracer gas as an odor source, emitted from a 0.014 m diameter copper tube 2 meters above the ground at a pressure of 10 PSI. We developed a mobile sensor stack consisting of a photo-ionization detector to record odor concentration, a GPS RTK receiver to record position, and an IMU to measure angular velocity (Fig. 1B). We placed 7 wind sensors around the odor source to measure the ambient wind direction and speed, and traversed this 60x60 m^2 space by foot while carrying the sensor stack for 6 hours (Fig. 1C).

The horizontal wind speed and direction were spatially consistent throughout the duration of the experiment (Fig. 1D), with comparatively low magnitudes of vertical wind (Fig. S1A). In subsequent analyses we used the closest stationary wind sensor to the odor source to represent the ambient wind speed and direction. Over the course of the day, the wind transitioned from low speeds and high directional variability to a strong southerly flow, indicating a shift in the local wind regime. We split our data into two datasets accordingly: "low wind speed" (LWS) < 3.5 m/s, and "high wind speed" (HWS) > 3.5 m/s (Fig. 1D).

The high variability in wind direction in our LWS and Forest environments would have resulted in very few encounters with the odor plume if we had used a stationary odor sensor, or one guided by entirely random movements. Instead, we used our real-time odor concentration signal to drive audio cues allowing us to center our walking trajectory around the plume to efficiently gather data about as many individual odor whiffs as possible. We attempted to follow trajectories reminiscent of the casting motifs exhibited by flying insects [12]. The majority of our movement was in the plane horizontal to the ground at walking speeds of 1-2 m/s. Our changes in direction in line with the source, and perpendicular to the source, ranged from 0.02-0.2 Hz (Fig. S2). For comparison, flies and moths cast at about 0.5-1 Hz=1-2 turns/sec [12, 33, 34]). We made small vertical movements on the scale of ± 0.5 m, generally staying aligned with the altitude of the source. Encounters with odors were infrequent: most of the time, our photo-ionization detector recorded values below 2 V, with occasional spikes in the readings (Fig. 1E). We established a threshold of 4.5V (2.2

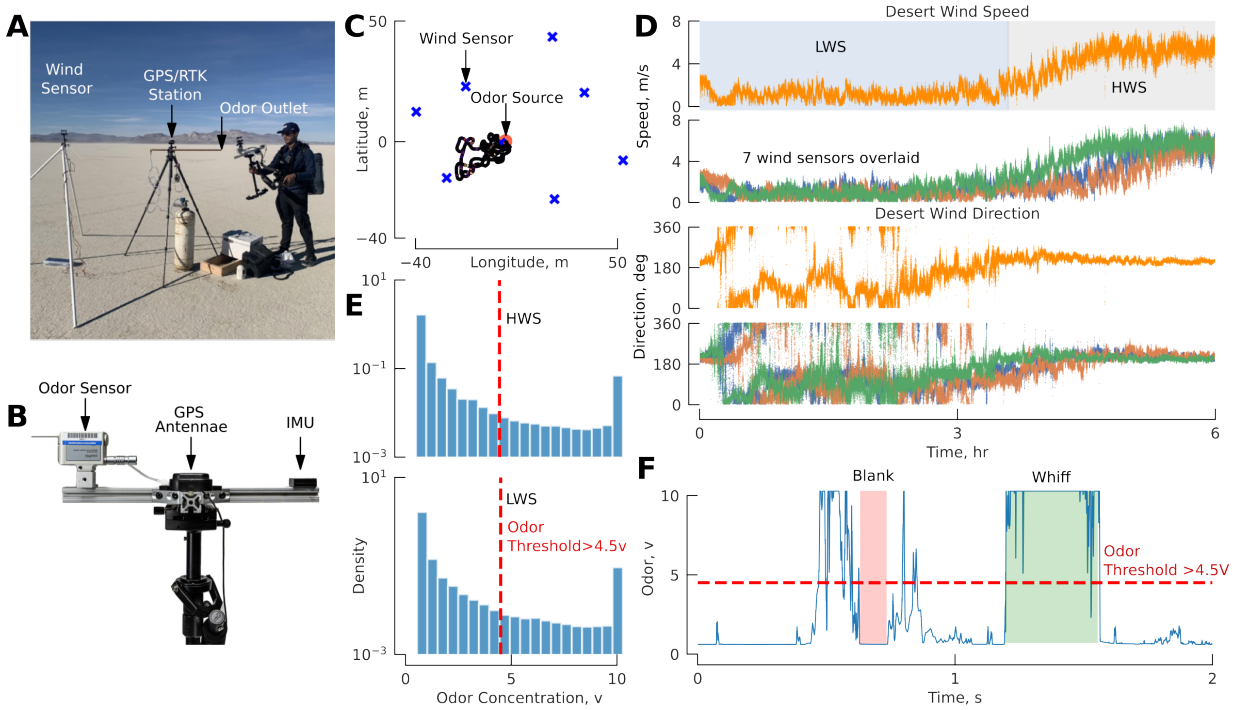

Figure 1: Experiment design: desert playa. **A.** Image from our Black Rock Desert field site showing the propylene odor source, GPS RTK antennae, one of seven ultrasonic anemometers, and gimbal supported sensor unit. **B.** Mobile sensor unit including a mini photo-ionization detector, GPS antenna, and IMU (Intertial Measurement Unit). **C.** Representative portion of our walking trajectory shown in relation to the odor source and anemometers. **D.** Wind speed and direction as a function of time for the duration of the 6-hour experiment for the anemometer closest to the odor source (orange traces), and all other anemometers (other colors). In our subsequent analysis we divided the data collected from this field site into two separate scenarios corresponding to the period characterized by low wind speeds and high directional variability (blue shading - HWS), and high wind speeds and low directional variability (gray shading - LWS). **E.** Log-scaled histogram of odor concentration recordings for this field site. **F.** Representative time trace of the odor signal, illustrating the intermittent nature characterized by whiffs (contiguous odor encounters greater than the 4.5 V threshold) and blanks (times when the odor signal was below the threshold).

times the standard deviation (σ) of all odor measurements) to categorize odor signals as either *whiffs* or *blanks* (Fig. 1F).

For our second environment we chose the Whittell Forest along Eastern Sierra Front in Nevada (Fig. 2A,B). We used a similar experimental arrangement but with the wind sensors positioned in an L-shape (Fig. 2C). Although in this environment we did find a higher degree of spatial variability of the wind, overall trends were similar across wind sensors and we again chose the closest wind sensor as a reference for the ambient wind speed and direction (Fig. 2D). Again, vertical wind speed was comparatively low (Fig. S1B).

Distribution of odor whiff locations is driven by wind characteristics

Before analyzing the correlation between odor statistics and distance to the source, we wanted to visualize the shape of the odor plumes in each condition. Because the wind direction varied throughout the course of our experiments, we developed an approach to "straighten" the data by aligning encounters relative to an ideal streakline. We determined the ideal streakline by integrating the wind velocity vectors over time. Figure 3A shows six snapshots of this moving streakline evolving over time. For each moment in time, we determined the shortest distance from the sensor location to the streakline centerline, and the distance from the sensor to the source. These two values allowed us to project sensor locations into a new streakline-centered coordinate frame (Fig. 3B).

Figure 3C shows the streakline-centered locations where we encountered odors for all three scenarios. In the high wind speed (HWS) dataset from the desert playa, the plume was quite narrow with odor encounters occurring close to the ideal streakline, and becoming rare at distances of 25 m away (Fig. 3Ci). For the low wind speed (LWS) dataset, odor

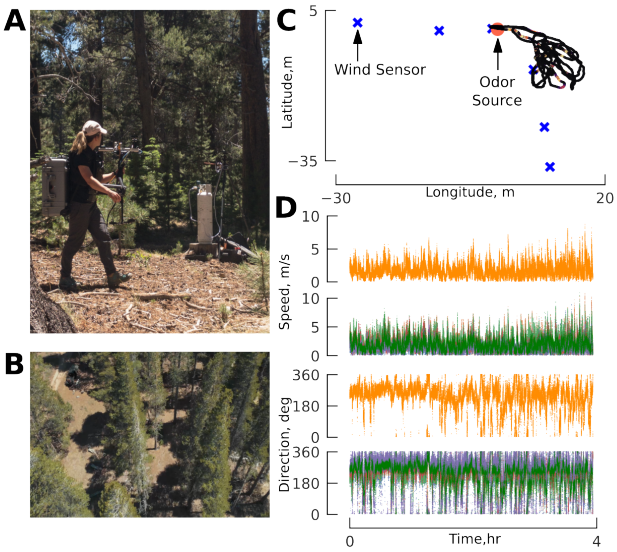

Figure 2: Experimental design: forest. **A.** We collected data by traversing the area surrounding the odor source on foot. **B.** Aerial view of the field site illustrating the tree density. **C.** Representative portion of our walking trajectory around the odor source, and arrangement of the ultrasonic anemometers. **D.** Wind speed and direction as a function of time for the anemometer closest to the odor source (orange traces), and all other anemometers.

encounters were spread out away from the streakline center much more widely (Fig. 3Cii). For our forest dataset (Fig. 3Ciii), odor encounters were mostly found within a smaller 10-15 meter radius from the source and did not have the same cone-like shape seen in the desert datasets. This could be because the wind was more variable due to the trees spread throughout the area. In each case, examples of both low and high concentration encounters can be found across the extent of the plume, though high concentration encounters were more frequent closer to the source.

Odor whiff statistics for estimating distance to source

To test if odor signal statistics are correlated with distance from the source, we calculated the following odor statistics (Fig. 4): whiff duration (wd), mean concentration during a whiff (wc), whiff frequency (wf, following calculations from [4], see Materials and Methods), whiff moving average (wma), and whiff standard deviation (wsd) of the encounters during a whiff. We define a single (average) value for each statistic for each individual whiff, resulting in the stepwise constant plots shown in Fig. 4B-F.

Table 1: $\boldsymbol{R^2}$ and semi-partial r for Distance $\sim$ Odor Statistics
Note: * for $1e^{-5} < p < 0.05$, ** for $p < 1e^{-5}$

		semi-partial r (% contribution)				
Dataset	R^2	wc	wf	wd	wma	wsd
Desert (HWS)	0.14	44.03 **	29.17 **	5.02 *	3.41 *	5.45 **
Desert (LWS)	0.13	70.53 **	7.98 **	26.72 **	0.03 *	0.48 *
Forest	0.08	81.29 **	1.97 *	22.10 **	1.21 *	0.21 *
All Combined	0.13	89.44 **	10.03 *	24.87 **	1.43 *	1.37 *

Individual whiff statistics are not strongly correlated with distance

To identify potential correlations between our selection of odor statistics and distance from the source, we constructed a multiple linear regression model for each of the three scenarios (Table 1, see S3 for residual analysis). We found whiff concentration and frequency to be the most significant statistics, but both had very subtle correlations with distance. Because we collected data by moving the sensor in a biased manner, we also considered the effects of our motion relative to the instantaneous wind direction, but did not find any meaningful difference in the results (Table **??**). Although we found individual whiff statistics to be poorly correlated with distance, the distributions of these

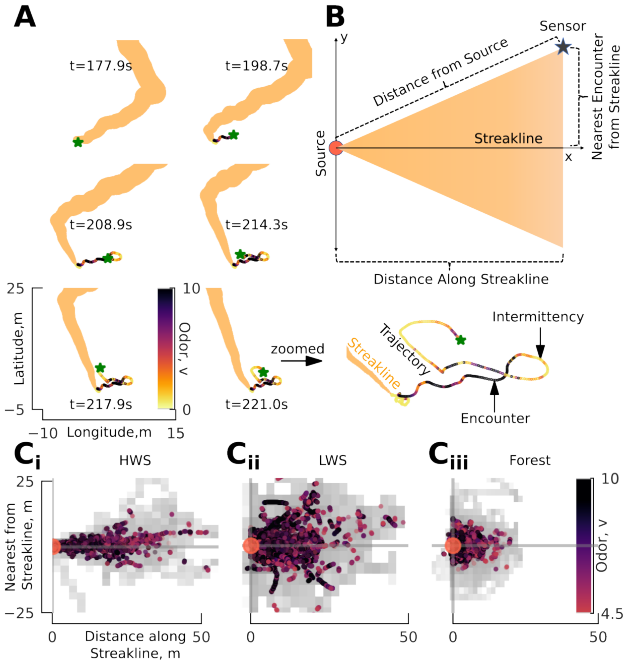

Figure 3: Streakline-aligned odor encounters reveal approximate shape and extent of the outdoor odor plumes. **A.** Six snapshots spanning 43 seconds showing the ideal streakline (orange, determined by integrating the ambient wind vector), together with our walking trajectory color-coded by the odor concentration recorded at each location. Green star indicates the location of the sensor for the same moment that the streakline is shown. The width of the streakline is for illustration purposes, not drawn to scale. **B.** To visualize the extent of the plumes despite the time varying wind direction we transformed each point along the trajectory from latitude/longitude to streakline coordinates. We calculated the distance from the sensor to the source and the shortest distance to the streakline. **C.** Using the approach described in **B**, we transformed each whiff (i.e. when the odor signal was > 4.5 V) into streakline coordinates for each of the three scenarios. Gray shading indicates time spent in streakline coordinate space, where darker shade indicates time spent more than 10 seconds. For a more clear histogram of time spent please refer to figure S4.

statistics (Fig. 4G) do exhibit consistent patterns in relation to distance. For example, whereas concentration of an individual whiff might be high, or low, across a wide range of distances, the distribution of whiff concentrations clearly trends to smaller values at higher distances. At larger distances whiff frequencies were more likely to be higher, thus high frequency but low concentration seqeuences of whiffs should be expected at large distances. At shorter distances, whiffs were rare (low whiff frequency), but when they did occur, they had a relatively long whiff duration and high whiff moving average. Finally, the overall pattern of the whiff standard deviation bears some resemblance to the whiff concentration, a relationship we explore more later. In the next section, we examine how the distribution of a time history of whiffs is correlated with distance.

A short time history of whiff statistics reveals strong correlations with distance

In this section, instead of considering individual whiff statistics, we collect all the whiffs that occurred within a short "lookback" time window (e.g. a trajectory snippet) and explore how meta statistics of this small collection of whiff statistics are correlated with the average distance from the source for that trajectory snippet. In some cases our trajectory snippets spanned a wide range of distances. To minimize the artifacts such snippets would create, we first split the datasets from each of our three scenarios into three distance classes (0-5m, 5-30m, and >=30 m). We randomly selected a total of 500 random trajectory snippets from each distance class, ensuring that each trajectory snippet was unique to a single region.

To characterize the distribution of whiff statistics for each trajectory snippet we chose five meta statistics: *min*, *max*, mean (μ), standard deviation (σ), and kurtosis (k), and applied these meta statistics to each of the five whiff statistics discussed previously. We first looked for correlations between these 25 inputs and distance to the source for a range of lookback times. We found a sharp increase in R^2 for lookback times from 1-5 seconds, with a continued but modest

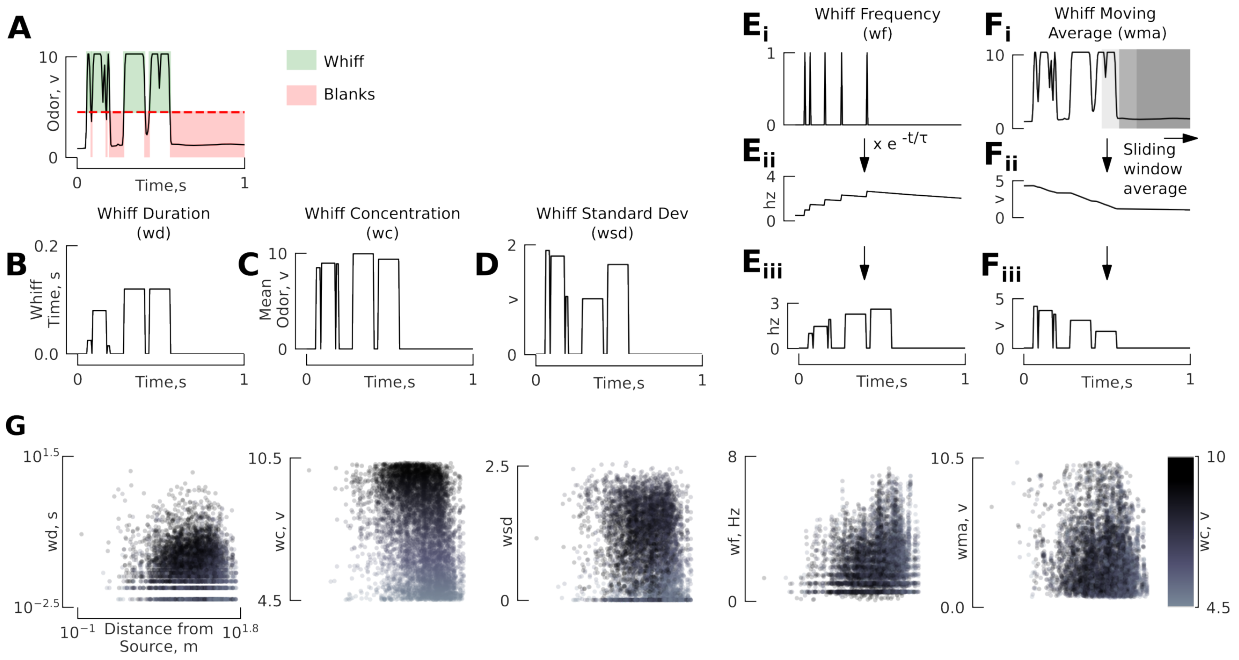

Figure 4: Individual whiff statistics are not strongly correlated with distance. **A.** Representative trace of odor concentration over time, color coded according to whiffs and blanks. **B-D.** For each individual whiff we calculate a single value corresponding to the whiff duration (wd), mean whiff concentration (wc), and standard deviation of the concentration within a whiff (wsd), resulting in piecewise constant time traces. **E.** Whiff frequency (wf) is calculated by convolving an exponential decay kernel ($\tau = 2$) with a binary delta function corresponding to the onset of each whiff. Each whiff is assigned a single value for the whiff frequency. **F.** We calculated the moving average of odor concentration using a sliding window (1 sec), and then assigned each whiff a single value corresponding to the mean of the moving average signal during the time frame of the whiff (wma). **G.** Statistics of individual whiffs are not strongly correlated with distance to source. Each panel shows a scatter plot of the whiff statistics defined above for all three scenarios combined. Color encodes the whiff concentration. Whiff statistics for the three scenarios are shown separately in Fig. S5.

increase for lookback times up to 10 seconds resulting in final R^2 values at 10 seconds ranging from 0.38 to 0.82 (Fig. 5A). Figure 5 panels B-F show how the mean of the five whiff statistics are correlated with distance, revealing that the mean of whiff concentration and mean of the standard deviation of each whiff both exhibit significant and strongly predictive correlations (Table S3).

Concentration and timing meta statistics are correlated with source distance

Next, we set out to understand which meta statistics of our whiff statistics provide the most predictive power for distance from the source. We chose to focus on a lookback time of 10 seconds for the rest of our analysis, as beyond this point R^2 does not substantially improve. We combined datasets from desert and forest environments and individually correlated the 25 meta statistics with distance (Fig. **??**). To compare the relative quality of different models and avoid overfitting we used Akaike's Information Criterion (AIC) [35] to construct a series of statistical models with increasing complexity (Table 2). To avoid overfitting, AIC penalizes models with more parameters, while rewarding those that fit the data well. The single most informative meta statistic was the mean whiff concentration. Small improvements in R^2 and AIC were realized as more meta statistics were included in the model, but after approximately 4 meta statistics the changes in AIC (ΔAIC) resulted in diminishing returns. With 4 parameters, the lowest AIC identified $\mu(WC)$, $\sigma(WD)$, $max(WMA)$, and $\sigma(WMA)$ as the most informative meta statistics for estimating distance.

Notably missing from the list of meta statistics selected by our AIC analysis is $\mu(WSD)$, which is strongly correlated with distance (Fig. 5F). This is because $\mu(WC)$ and $\mu(WSD)$ are mutually correlated (Figure S6, $R^2 = 0.51, p = 4.61e^{-228}$), so including $\mu(WSD)$ in a statistical model that already contains $\mu(WC)$ does not provide enough novel

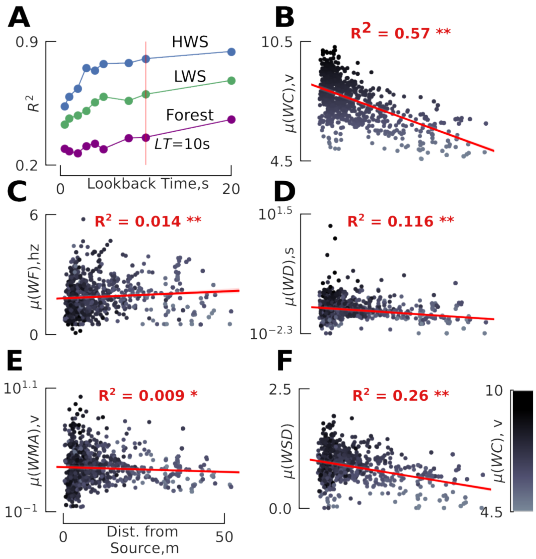

Figure 5: Meta statistics for whiffs occurring within a 10 second "lookback" time window are strongly correlated with distance from the source. **A.** For the collection of whiffs occurring within a chosen lookback time for randomly sampled trajectory snippets (see text) we calculated five meta statistics: mean, standard deviation, min, max, and kurtosis of each of our whiff statistics. The correlation coefficient for a linear regression relating these 25 meta statistics to the source distance rises with increasing lookback times. In subsequent analyses we chose to focus on a lookback time of 10 seconds. **B-F.** Distribution of the mean of each whiff statistic with respect to the distance from the source for a lookback time of 10 seconds. Here data are combined across all three scenarios. Red line shows the correlation, see Table S3 for detail.

Table 2: AIC and ΔAIC for selecting the most significant statistics that correlate with Distance from source

$min(AIC)$	ΔAIC	Parameters
10726.2	0	0
10655.9	-70.3	$\mu(WC)$
10631.2	-24.7	$\mu(WC)$, $\sigma(WMA)$
10594.5	-36.6	$\mu(WC)$, $\sigma(WMA)$, $max(WMA)$
10575.1	-19.5	$\mu(WC)$, $\sigma(WMA)$, $max(WMA)$, $\sigma(WD)$
10557.3	-17.8	$\mu(WC)$, $\sigma(WMA)$, $max(WMA)$, $\sigma(WD)$, $max(WC)$

information and would violate model assumptions, increase bias and skew the regression results. The strong correlation between $\mu(WC)$ and $\mu(WSD)$ suggests that these two meta statistics are somewhat interchangeable.

To compactly visualize all strongly correlated groups of meta statistics we constructed a hierarchically clustered matrix of the correlations between each pair of meta statistics (Fig. 6). The resulting adjacency matrix identifies $\mu(WC)$ and $\mu(WSD)$ as their own cluster (Fig. 6A), suggesting that these interchangeable statistics provide unique information compared to other whiff statistics, and that the mean and variability (WC and WSD, respectively) within a whiff are related. Both meta statistics decrease with increasing distance (Fig. 5B,F), perhaps because at larger distances diffusion has had a chance to both even out the odor distribution and reduce the concentration within a whiff. Overall this cluster can be summarized as one that captures concentration information.

Our AIC analysis also identified $\sigma(WD)$,$max(WMA)$, and $\sigma(WMA)$ as informative, and we find that these whiff statistics form their own cluster in the adjacency matrix (Fig. 6B). Because longer whiff durations will typically result in larger whiff moving averages, this cluster can be summarized as one that captures variability in whiff duration (and its maximum), e.g. a measure of odor timing.

The next clear cluster (below and right of B) includes meta statistics that describe the variability of both whiff concentration and standard deviation across whiffs. Although these meta statistics are correlated with distance, our AIC analysis suggests variability of these concentration related statistics may not be as informative as their mean (note the correlation between this cluster and cluster A).

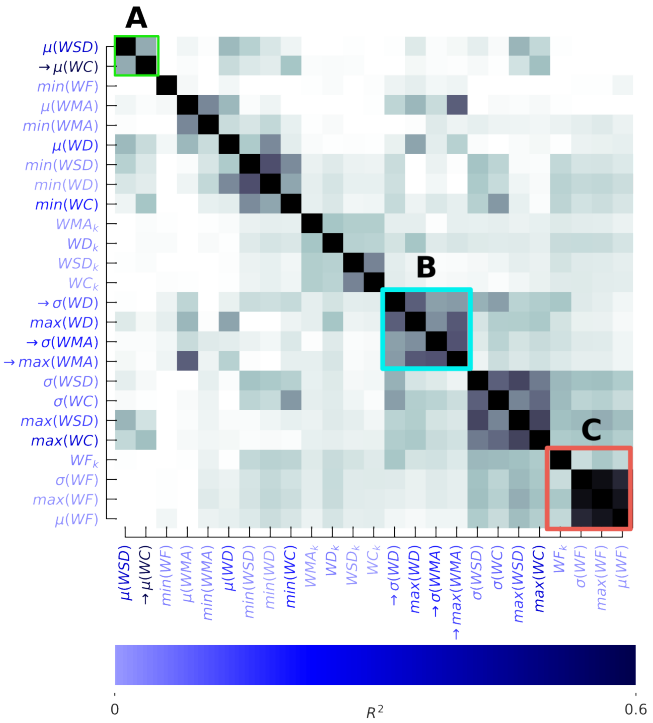

Figure 6: Hierarchical clustering reveals distinct clusters of mutually related meta statistics of whiffs within a lookback window. Darker colors in the adjacency matrix correspond to higher pairwise correlations between meta statistics. The R^2 correlation coefficient between each individual meta statistic and distance to the source is encoded in the blue shading of the meta statistic labels. Arrows indicate meta statistics selected by the 4-parameter model from Table 2. **A** Concentration related parameters $\mu(WC)$ and $\mu(WSD)$ are mutually correlated (see also Fig. S6), and are both strongly correlated with the source distance (see also Fig. **??**A). **B**. The parameters related to whiff duration – $\sigma(WD)$, $max(WMA)$, and $\sigma(WMA)$ – form a distinct group, three of which are also selected by the AIC analysis. **C**. Whiff Frequency meta statistics form a cluster and provides unique information about the distance to the odor source, albeit low correlation with distance to the source.

Finally, we see that meta statistics of whiff frequency form a distinct cluster (Fig. 6C), indicating that whiff frequency provides unique odor timing related information compared to our other whiff statistics. However, whiff frequency is not strongly correlated with distance in our experiment (Table S3, $R^2 = 0.014, p = 4.0e^{-06}$). We discuss this apparent conflict with existing literature in the discussion.

Integrating whiff statistics with relative motion can provide a continuous estimate of source distance

The intermittent nature of odor whiffs means that any estimate of distance based solely on whiff statistics will also be highly intermittent, and therefore of limited utility. To illustrate how this signal could be used to generate a continuous estimate of distance we used a constant velocity Kalman smoother (see Materials and Methods). Our Kalman smoother integrates two measurements. First, we use the intermittent distance predictions from our AIC filtered 4-parameter statistical model that combined data from all three scenarios given by the following equation,

$$\text{distance} = -8.85\mu(WC) + 0.20\max(WMA) - 2.43\sigma(WMA) - 3.07\sigma(WD) + 84.40 \tag{1}$$

Second, we use continuous estimates of the sensor ground velocity (acquired via GPS) component parallel to the instantaneous ambient wind direction. Despite the model simplicity, our smoothed continuous distance estimates produced surprisingly accurate distance estimates in both the desert HWS and LWS scenarios, achieving median errors in absolute distance of 3.9 m and 6.26 m, respectively (Fig. 7A-B). For the Forest scenario, our estimates consistently overestimated the true distance, resulting in a median error of 7.76 m (Fig. 7C). These estimates can be

slightly improved by using statistical models that are tailored to each specific environment, but the improvements in performance are modest (Fig. S8).

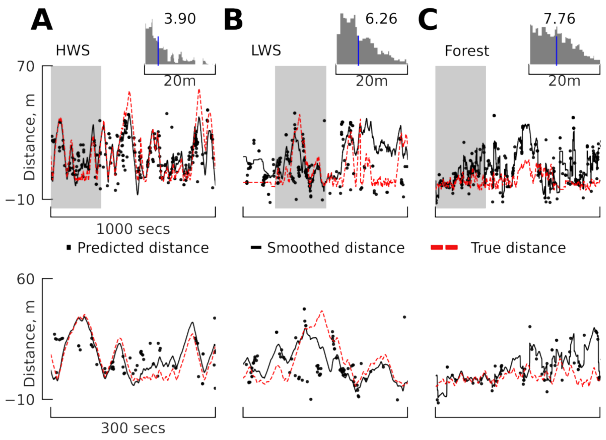

Figure 7: Integrating whiff statistics with relative motion in a Kalman smoother yields continuous estimates of source distance. **A-C** Upper row: Comparison of predicted, Kalman smoothed, and true distances for three scenarios. Our Kalman smoother combined intermittent distance estimates from our combined desert+forest linear model with continuous estimates of our ground velocity component parallel to the ambient wind. Histograms show the median error between the Kalman smoothed and true distance. Lower row: a magnified view of the shaded regions from the upper row. For an even zoomed-in presentation of the above smoothed results and if environment-specific prediction models are used, refer to Figure S8.

Odor Signal Temporal Resolution needs to be upwards of 20Hz for accurate distance estimation

Finally, we asked whether a high temporal resolution of the odor signal is necessary to accurately estimate the distance to the source, or if slower time-averaged measurements would perform equally well.

To answer this question, we low-pass filtered our 200 Hz odor signal time series using a 2nd order Butterworth filter [36]. Figure 8A shows representative time traces of the filter's effects. For each cutoff frequency, we re-ran our analysis pipeline to identify the new whiffs, their statistics, the meta statistics for a 10-sec lookback window and calculated the R^2. Our results show cutoff frequencies of less than 20 Hz generally result in substantially reduced predictive power (especially in the HWS and Forest scenarios) (Fig. 8B). The variability–and sometimes apparent improvement in performance–in the R^2 metric in the 2-8 Hz is likely an artifact resulting from the small number of whiffs that remain under these extreme filtering conditions.

Discussion

Summary

We conducted experiments in three outdoor scenarios to determine if odor whiff statistics could be used to estimate the distance of a plume source at large spatial scales. We found that statistics from individual whiffs are poorly correlated with distance (Fig. S5), with the whiff concentration and whiff frequency being the best features. Meta statistics constructed from a 10-second time history of whiffs, however, were strongly correlated with distance. A hierarchical clustering analysis of these meta statistics revealed two distinct clusters of mutually correlated meta statistics that were also strongly correlated with distance. These clusters correspond to concentration features (the mean concentration and standard deviation of concentration within a whiff, Fig. 6A), and timing features (whiff duration and moving average, Fig. 6B). Whiff frequency formed its own distinct cluster, but contrary to its correlation with distance with individual whiffs, none of the meta statistics of whiff frequency were strongly correlated with distance (figure 6C). The correlation between whiff statistics and distance was strongest ($R^2 = 0.8$) in our most uniform scenario (high wind speed with low directional variability), and with an odor sampling frequency of 20 Hz or more.

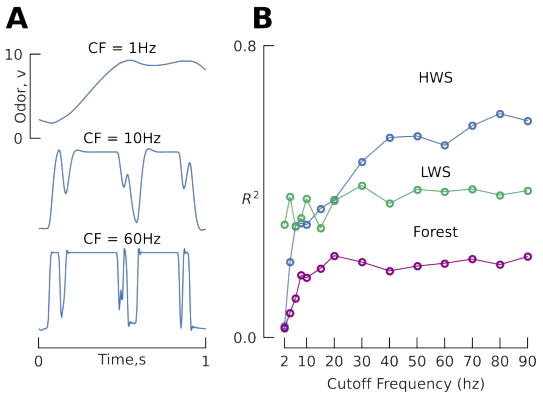

Figure 8: Low pass filtering odor signal degrades correlations between whiff statistics and source distance. **A**. Sample time traces of odor signal for selected cutoff frequencies used in a 2nd order Butterworth filter and varied the cutoff frequency from 1 Hz to 90 Hz (approximately half the Nyquist frequency), while keeping the order of filter constant at two. **B**. The correlation coefficient for distance correlated with AIC filtered whiff meta statistics for a lookback time of 10 seconds as a function of cut-off frequency (CF).

Comparison with prior work

With one important exception, our field study results are broadly consistent with prior efforts aimed at understanding how odor statistics relate to source distance at much smaller spatial scales. Rigolli et al.[28] used high fidelity fluid dynamics simulations on scales of a few meters to show that odor statistics related to concentration and timing provide complimentary distance information. Furthermore, their results indicate that at greater distances where encounters are more rare, concentration features are better predictors, consistent with our results. In wind tunnel experiments, [2] and [3] found the distribution of whiff frequency to be correlated with distance from the source, and in the experiments by Demir et al. [4], whiff frequency proved to be a major factor that influenced walking flies' decision to turn upwind. In our experiments, however, whiff frequency provided limited predictive power compared to whiff duration in both our lookback analysis (Fig. 6), and for individual whiffs in the dynamic wind scenarios (LWS, Forest, see Table 1). Only for individual whiffs in the HWS case was whiff frequency more predictive compared to whiff duration, though its utility was still limited ($R^2 = 0.04$). Together, our results are consistent with the idea that for a sensor that is moving slowly relative to wind, whiff frequency may carry useful information. However, under more naturalistic conditions that involve either dynamic wind, or a moving sensor that may or may not stay within the odor plume envelope, whiff frequency may be an unreliable cue when accumulating evidence over a longer lookback window, and the duration of individual whiffs may be more informative.

Experimental limitations

Our field experiments were necessarily limited due to the logistics of gathering this type of data. Accordingly, we chose to use a single source geometry, odorant, release concentration, and flow rate for all three scenarios. The specific values of the coefficients relating distance to each of the whiff statistics we considered would likely change for different choices of these parameters. However, the modest improvement in distance estimation accuracy we achieved when considering environment specific models instead of a single combined model suggests that distance estimation can be relatively robust to specific characteristics of the environment. Furthermore, our hierarchical clustering analysis suggests that robustness to differences in release concentrations may be realized by relying on the standard deviation within a whiff more so than the concentration.

Implications for plume tracking insects and robots

As a result of turbulence in natural wind, as well as dynamics of an agent's own motion, any agent tracking an airborne odor plume will experience a sequence of whiffs that are highly intermittent. We showed that by incorporating statistics from these intermittent signals over a time history with the help of a Kalman smoother it is possible to generate a continuous estimate of distance to the source (Fig. 7). The accuracy of these distance estimates (3-8 meters depending on the environment) is in line with the range over which insects such as mosquitoes are likely to begin resolving potential odor sources [5, 6], making it a practically useful estimate for potentially gating the behavioral decision to

approach those visually salient features. However, achieving an accurate estimate of distance requires high temporal resolution of the olfactory experience of at least 20 Hz. This is consistent with the timescale of olfactory coding in insects [37]. Rough estimates of distance could be used for modulating decisions such as casting amplitude, or when to initiate a local search, both of which may improve search efficiency for machines and animals alike.

Do plume tracking animals make estimates of their distance to an odor source, and use that to adjust their plume tracking decisions? At small spatial scales, walking flies do adjust their decisions based on whiff frequency [4]. Less is known about how whiff statistics modulate behavior at larger spatial scales. However, experiments with moths and flies suggest that even on spatial scales of a meter or so, the fine details of plume tracking decisions are influenced by spatial and temporal memory of the odor experience [20, 38]. Meanwhile, virtual agents trained to track simulated plumes show an improvement in performance when they have access to a memory of odor and wind time history [39]. In neither case is it clear whether agents use an estimate of source distance to drive their modulation of behavior. Our data, however, suggests that this is a distinct possibility. We predict that for flying agents, whose olfactory experience will be influenced by their own trajectory more so than slower moving walking agents, whiff concentration and duration may be the primary features that animals integrate over timescales of 5-10 seconds to generate a rough internal estimate of distance. Experiments with flying mosquitoes interacting with a CO_2 plume indicate that odor can influence their decision to approach visually salient objects on these timescales [5]. Rigorously testing our hypothesis will require a detailed analysis of how whiff concentration and duration modulate decisions such as approaching visual objects, or casting behavior. Recently developed approaches for delivering precisely controlled olfactory stimuli using optogenetics make it feasible to now test this hypothesis [21].

Experimental Setup

Black Rock desert setup

The setup can be divided into two components, the first being the mobile sensor stack that was carried by a human for collecting odor signals, and the second component included the placement of 8 stationary wind sensors for ambient wind measurements around the odor source. The odor source was a propylene gas tank (figure 1A) that was mounted with a stationary GPS antenna which sent Real Time Kinematics (RTK) correction data to the mobile sensor stack (ublox ANN-MB-00-00 Multiband GNSS Antenna connected to a ublox ZED-F9P receiver attached with an RN41 Bluetooth module for pairing with a Dell Laptop running ROS in Ubuntu Linux OS), which together provided high-resolution position with an accuracy close to 1cm.

The mobile sensor stack in Figure 1B included a mini photo ionization detector (200B miniPID photo-ionization detector, Aurora Scientific), a GPS antenna (with the same ublox receiver Bluetooth module as above) to receive accurate location measurements, and an IMU that provided angular velocity measurements. The sensor stack was balanced on a gimbal for stability and ease of carrying. The odor sensor data was collected using a data acquisition board (MC Measurement Computing-USB1608GX), which was connected along with all the other sensors to a computer that was running ROS as middleware and recorded data in real time. Due to the different sampling rates of sensors (wind sensors: 40 Hz, GPS: 5 Hz), the data were linearly interpolated with respect to the rate of the odor sensor which sampled at 200 Hz.

Around the odor source, 7 ambient wind sensors (LI-550F TriSonica Mini Wind and Weather Sensor, Trisonica/Li-Cor) were placed 2 meters above the ground in a square fashion approximately 30 meters away from the source, and one other wind sensor was placed 1 meter away from the odor source for accurate measurement of wind speed and direction near the source as in Figure 1A, C.

Whittell forest setup

A similar arrangement of odor source and wind sensors was set up in Whittell Forest to collect odor encounter data under a forest canopy as in Figure 2A and 2B. The array of sensors was placed in an L-shaped fashion to better sample the heterogenous environment (Fig. 2C).

Calculating whiff frequency (wf)

Whiff Frequency is a representation of how often a whiff was encountered within a given duration of time. Following previous applications of whiff frequency in related studies, we used a 1 second time window for calculating whiff frequency [4]. We converted the time series of odor signals to a binary sequence of delta functions, resulting in a time trace that was zero everywhere except for the first frame of each whiff which were assigned a value of 1, see Figure $4E_{(i)}$. We convolved this sequence of whiff onsets with an exponential filter to determine the whiff frequency:

$$W_{freq}(t) = \int_0^t w(t')g(t-t')dt', \tag{2}$$

where $w(t')$ is the binary whiff onset signal, t' is the time at which we are calculating the whiff frequency. The kernel function g is defined as follows,

$$kernel(t') = \begin{cases} \frac{1}{\tau}e^{-\frac{1}{\tau}(t-t')} & \text{for } t < 1 \\ 0 & \text{for } t > 1 \end{cases}, \tag{3}$$

where τ is the decay constant, a measure of how long the previous whiff should be remembered. Based on the whiff data and time constants chosen in [4], we chose τ = 2 sec (Fig. 4 $D_{(ii)}$). To calculate a single whiff frequency value for each whiff, we averaged the whiff frequency across each individual whiff.

Kalman Filtering

We calculated a continuous estimate of distance to the odor source using a Kalman smoother [40]. We defined a linear and time-invariant discrete dynamical systems model,

$$\begin{aligned} \boldsymbol{x}_{k+1} &= A\boldsymbol{x}_k + B\boldsymbol{u}, \\ \boldsymbol{y}_k &= C\boldsymbol{x}, \end{aligned} \tag{4}$$

where $\boldsymbol{x}$ describes two states: the distance to the source, and the velocity towards or away from the source. For simplicity, we did not include any control inputs in our model, instead accounting for this modeling uncertainty in our covariance matrix Q, resulting in a simple constant velocity dynamic model,

$$A = \begin{bmatrix} 1 & dt \\ 0 & 1 \end{bmatrix}, \qquad B = \begin{bmatrix} 0 \\ 0 \end{bmatrix}, \qquad C = \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix}.$$

In a real-world application of an agent searching for an odor source, neither of the states we defined can be directly measured (because the source location is unknown). Thus, for our measurements we used the following two (imperfect) observer models to estimate a proxy for these states that are then incorporated into the Kalman smoother. We account for the uncertainty resulting from this discrepancy through our measurement covariance matrix R. We calculated an estimate of the distance using our combined regression model (Eqn. 1) to make an intermittent distance prediction associated with each whiff, based on the lookback time of 10-seconds. We also compared the performance of distance estimates when using scenario-specific regression models (Fig. S8). We estimated the velocity towards or away from the source by calculating the sensor's ground speed component that was parallel to the current ambient wind direction.

For the HWS and LWS scenarios, we defined the measurement and model covariances (R and Q) to account for the uncertainties in the measurements (R) and the dynamic model (Q) as follows:

$$R = \begin{bmatrix} 10^{-1} & 0 \\ 0 & 10^{-3} \end{bmatrix}, \qquad Q = \begin{bmatrix} 10^{-3} & 0 \\ 0 & 10^{-1} \end{bmatrix}.$$

For the Forest scenario, we were able to reduce the median error with slightly different covariance matrices, which help to account for the increase in variability of wind direction in that dataset:

$$R = \begin{bmatrix} 10^{-2} & 0 \\ 0 & 10^{-3} \end{bmatrix}, \qquad Q = \begin{bmatrix} 10^{-2} & 0 \\ 0 & 1 \end{bmatrix}.$$

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Supporting Information

Table S1: Comparison of $\boldsymbol{R^2}$ and relative motion adjusted $\boldsymbol{R^2}$ for individual whiff statistics when correlated with distance from source. To account for relative motion, we first determined the relationship between each whiff statistic and the sensor's velocity parallel and perpendicular to the wind: $\boldsymbol{wc} \sim v_{||} + v_{\perp}$. In our regression with source distance, we then used the residuals for each whiff statistic after removing the relative motion effects: $\boldsymbol{wc_r = wc - \alpha_1 * v_{||} - \alpha_2 * v_{\perp}}$

Dataset	Original R^2	Relative Motion Adjusted R^2
HWS	0.14	0.14
LWS	0.014	0.13
Forest	0.08	0.07
All Combined	0.13	0.13

Table S2: $\boldsymbol{R^2}$ and model significance (p-value) correlating distance from the source with all 25 meta whiff statistics collected over a lookback window = 10 seconds.

Dataset	R^2	$f - pvalue$
HWS	0.82	extremely small
LWS	0.61	$8.94e^{-226}$
Forest	0.38	$8.77e^{-65}$
All Combined	0.65	$1.67e^{-300}$

Table S3: $\boldsymbol{R^2}$ and p-value for individual meta whiff statistics for a lookback window of 10 seconds, correlated with distance from source

Parameter	R^2	$p - value$
$\mu(WC)$	0.57	$1.02e^{-266}$
$\mu(WF)$	0.014	$4.0e^{-06}$
$\mu(WD)$	0.116	$1.26e^{-40}$
$\mu(WMA)$	0.009	$3.41e^{-04}$
$\mu(WSD)$	0.26	$3.92e^{-98}$

Table S4: $\boldsymbol{AIC}$ and $\boldsymbol{\Delta AIC}$ for selecting the most significant statistics that correlate with distance from source (10 iterations).

$min(AIC)$	ΔAIC	Parameters
10726.2144	0	0
10655.8883	-70.3260	$\mu(WC)$
10631.1534	-24.7349	$\mu(WC)$, $\sigma(WMA)$
10594.5044	-36.6490	$\mu(WC)$, $\sigma(WMA)$, $max(WMA)$
10575.0510	-19.4534	$\mu(WC)$, $\sigma(WMA)$, $max(WMA)$, $\sigma(WD)$
10557.2739	-17.7770	$\mu(WC)$, $\sigma(WMA)$, $max(WMA)$, $\sigma(WD)$, $max(WC)$
10532.4997	-24.7742	$\mu(WC)$, $\sigma(WMA)$, $max(WMA)$, $\sigma(WD)$, $max(WC)$, $min(WC)$
10529.4179	-3.0818	$\mu(WC)$, $\sigma(WMA)$, $max(WMA)$, $\sigma(WD)$, $max(WC)$, $min(WC)$, WC_k
10524.6016	-4.8162	$\mu(WC)$, $\sigma(WMA)$, $max(WMA)$, $\sigma(WD)$, $max(WC)$, $min(WC)$, WC_k, $\mu(WMA)$,

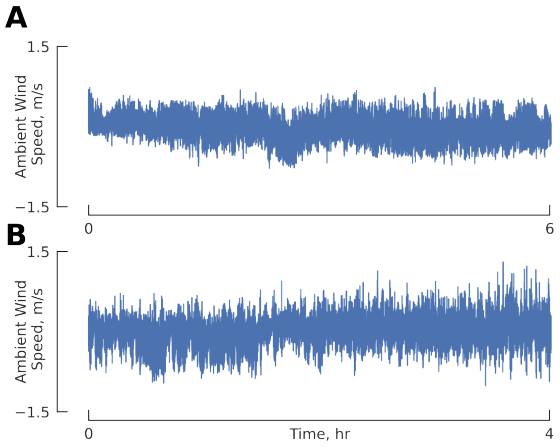

Figure S1: Vertical ambient wind velocity remained small and mostly constant throughout the experiment period in **A** the Desert and **B** the Forest

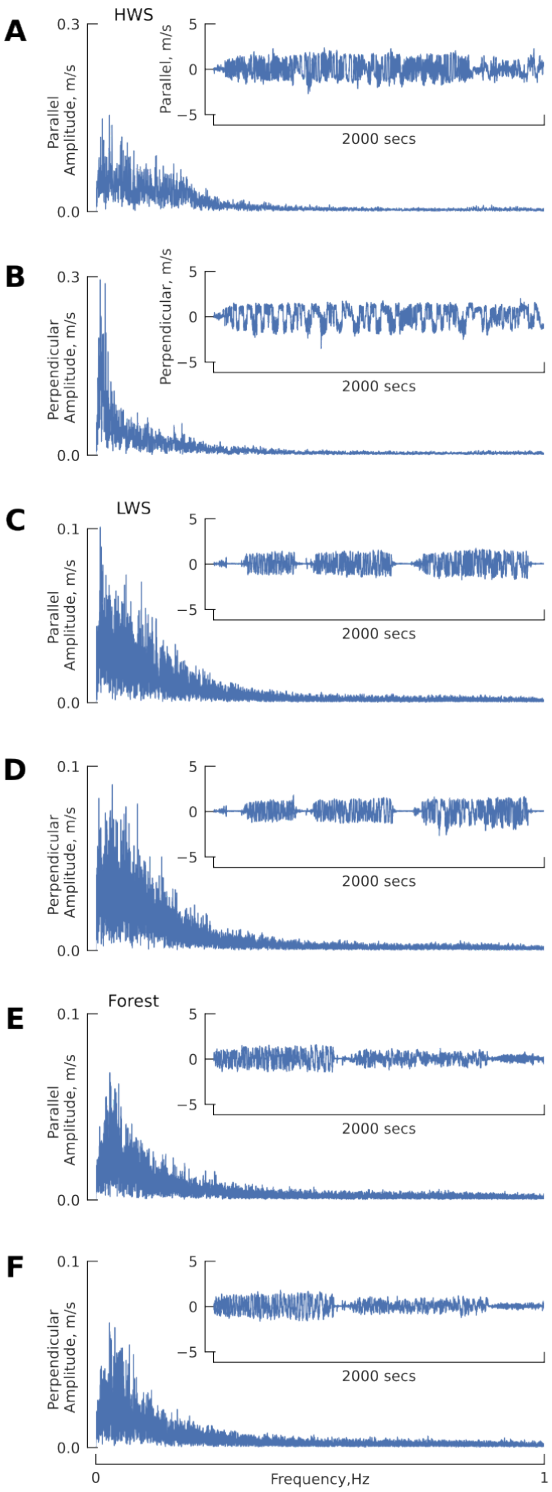

Figure S2: Sensor ground velocity (from GPS measurements) projected onto the unit vector pointed towards the source (parallel component) or perpendicular to that direction. Insets show raw time series plots of these velocities, and the larger plots show the FFT of each component. **A-B** HWS, **C-D** LWS, **E-F** Forest datasets. Dynamics similar to casting are best seen in the HWS scenario, where we made more frequent movements perpendicular to the direction pointing towards the source. In the LWS and forest scenarios we made more randomized movements to find the odor plume.

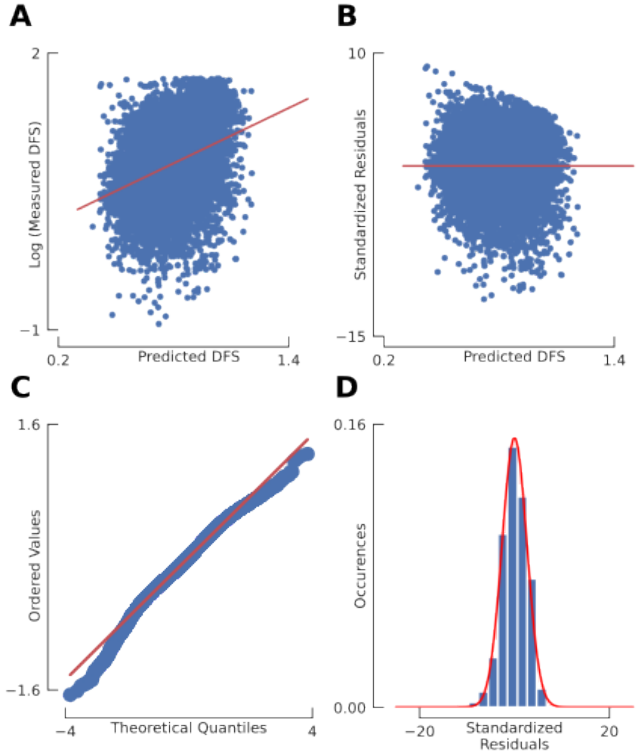

Figure S3: Comprehensive residual analysis for model validation **A.** Actual vs predicted. Scatter plot illustrating the correlation between the actual and predicted values, providing an overview of the model's accuracy. **B.** Standardized residuals. A plot of the standardized residuals helps identify any outliers that could potentially influence the model's performance. **C.** Residual analysis. Q-Q plot: A quantile-quantile plot used to assess if the residuals follow a normal distribution. **D.** Normality of residuals. A histogram with an overlaid normal curve to visually inspect the distribution of the residuals.

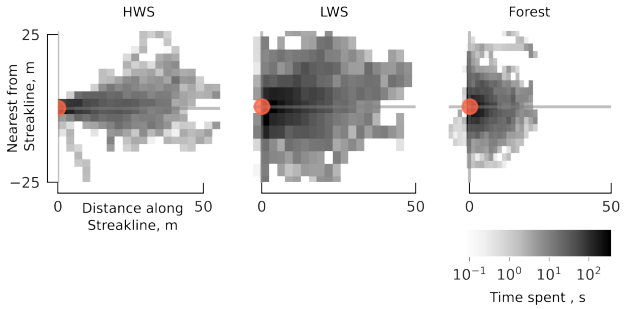

Figure S4: Using the coordinate system introduced in Figure 3B, this figure shows a representation of how much time the sensor was in each location relative to the streakline and odor source.

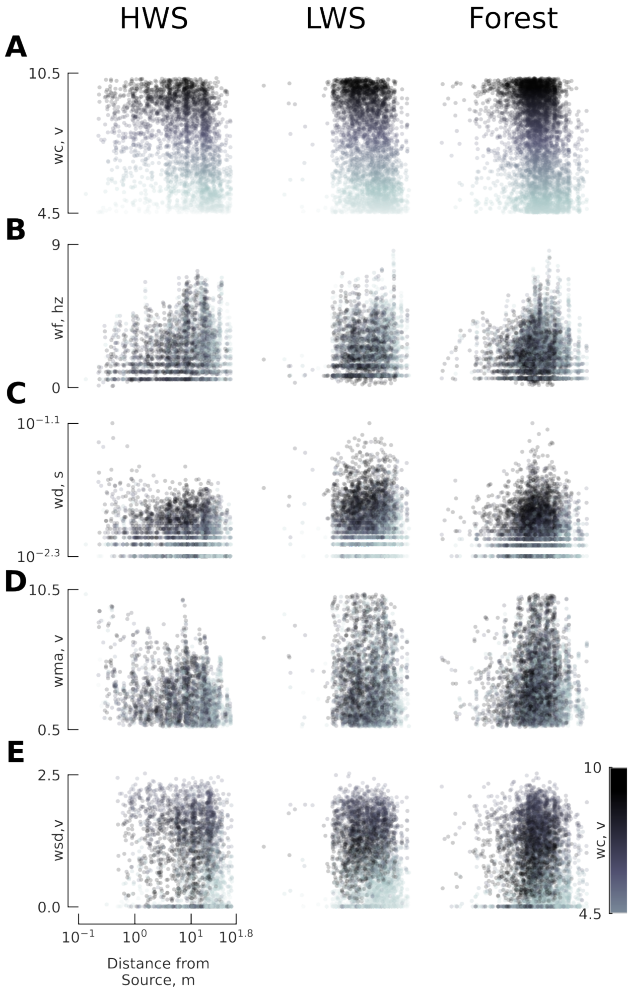

Figure S5: Individual whiff statistics vs distance from source for HWS, LWS and Forest (column wise) **A.** Whiff concentration **B.** Whiff frequency, **C.** Whiff duration, **D.** Whiff moving average **E.**Whiff standard deviation.

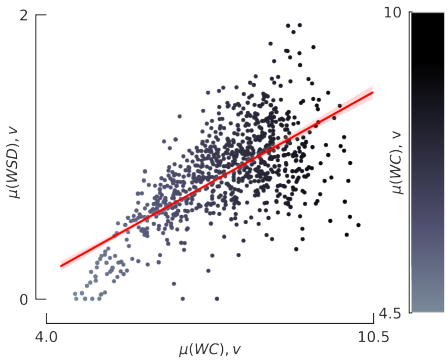

Figure S6: Relationship between meta statistics for the mean whiff concentration ($\mu(WC)$) and mean whiff standard deviation ($\mu(WSD)$). The trend line shows they are almost linearly correlated. This helps to explain why the ΔAIC analysis in table 2 did not select $\mu(WSD)$, even though it has the second highest correlation with distance from the source (Fig. **??**)

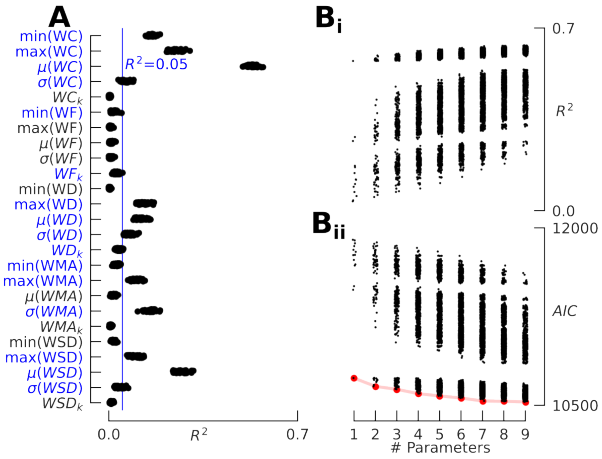

Figure S7: **A.** Bootstrapped R^2 is shown for each meta statistic. For subsequent analyses, we focus on meta-statistics that reached above a threshold of $R^2 = 0.05$ (blue). **B.** To find the most important meta statistics, we calculated the R^2 and AIC for all possible models containing up to 9 meta statistics. The red line in $\mathbf{B_{ii}}$ shows the best models.

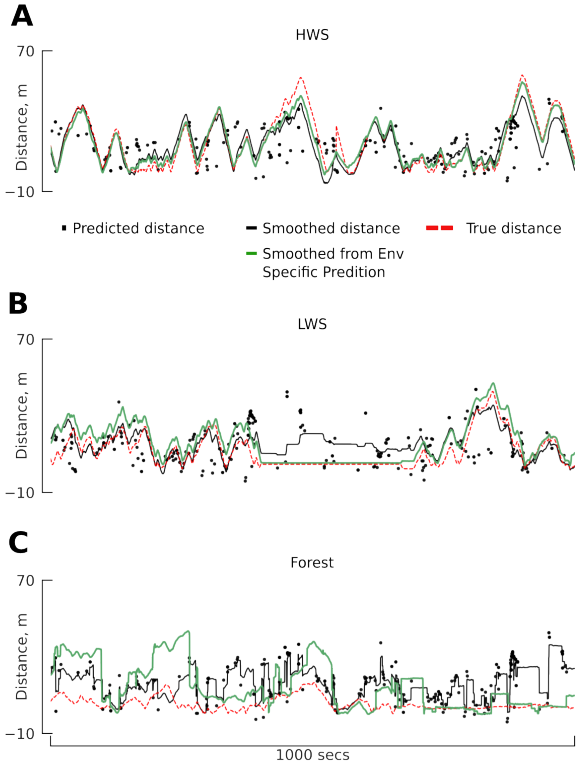

Figure S8: Kalman smoothed estimates of the distance to the odor source (red and black lines) vs intermittent distance predictions from our 4-parameter regression model for the 10-second lookback window (black dots) vs true distance (red dashed line), similar to Figure 7. The black lines (copied from Fig. 7) shows the smoothed distance estimates when using the same combined model for all three scenarios (distance $\sim$ model). The green lines show the smoothed distance estimates when environment-specific regression models are used: **A.** HWS (distance = -10.74 μ(WC) - 0.63 max (WMA) + 1.16 σ(WMA) - 7.45 σ(WD) + 102.47) **B.** LWS (distance = -7.59 μ(WC) + 0.52 max(WMA) - 0.82 σ(WMA) - 7.92 σ(WD) + 73.24) **C.** Forest (distance = -1.3 μ(WC) + 0.09 max(WMA) - 0.06 σ(WMA) - 0.53 σ(WD) + 15.05).