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Original Article

How Ambient Environment Influences Olfactory Orientation in Search and Rescue Dogs

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Abstract

Under natural conditions, an animal orienting to an air-borne odor plume must contend with the shifting influence of meteorological variables, such as air temperature, humidity, and wind speed, on the location and the detectability of the plume. Despite their importance, the natural statistics of such variables are difficult to reproduce in the laboratory and hence few studies have investigated strategies of olfactory orientation by mobile animals under different meteorological conditions. Using trained search and rescue dogs, we quantified the olfactory orientation behaviors of dogs searching for a trail (aged 1–3 h) of a hidden human subject in a natural landscape, under a range of meteorological conditions. Dogs were highly successful in locating the human target hidden 800 m from the start location (93% success). Humidity and air temperature had a significant effect on search strategy: as air conditions became cooler and more humid, dogs searched significantly closer to the experimental trail. Dogs also modified their speed and head position according to their search location distance from the experimental trail. When close to the trail, dogs searched with their head up and ran quickly but when their search took them farther from the trail, they were more likely to search with their nose to the ground, moving more slowly. This study of a mammalian species responding to localized shifts in ambient conditions lays the foundation for future studies of olfactory orientation, and the development of a highly tractable mammalian species for such research.

Key words: canine, cognition, meteorology, sensory ecology, spatial navigation

Introduction

Animals orienting to air-borne odor plumes must do so in constantly changing meteorological conditions, with humidity and temperature shaping plume characteristics. Because most studies of olfactory orientation are conducted on small species (e.g., insects and laboratory rodents) in captivity, there is of a dearth of field studies. Thus, how animals adapt to the changing physical properties of the plume in the field is poorly understood (Vickers 2000; Baker et al. 2018). The olfactory landscapes faced by long-distance olfactory navigating vertebrates, such as homing and migrating birds or polar bears, have instead been estimated by proxy (e.g., pollutant particle movement, Wallraff 2013) or with models (Safi et al. 2016; Togunov et al. 2017).

How such conditions should affect air-borne odor characteristics is a complex question. Odors typically consist of multiple chemical constituents, most of which are low-molecular weight, volatile organic compounds (Auffarth 2013). Further, such complicated mixtures exist in multiple phases simultaneously: vapor, aerosol, and liquid, when deposited on a surface. Each potential reservoir may have a different chemical composition. Three important parameters determining this composition are air temperature, relative humidity, and wind speed. Thus, the odor stimuli available to a navigating animal is highly dynamic in space and time, due to both local atmospheric thermodynamic conditions (i.e., temperature and relative humidity) as well as local atmospheric flow conditions (i.e., velocity and variability). Finally, natural environments are best characterized as turbulent flow conditions; the chaotic velocity field is highly variable in time and space (Csanady 1973).

Search and hunting dogs are known to locate targets accurately over a range of meteorological conditions (reviewed in Rosell 2018). Yet it has been difficult to show exactly how weather influences a dog's search, since dogs are equally successful in finding the target under different weather conditions (Greatbatch et al. 2015). The question of how dogs adapt their search strategy to compensate for weather changes has not yet been addressed, despite a number of studies on search strategies (Thesen et al. 1993; Gazit et al. 2005; Hepper and Wells 2005). Our goal therefore was to test the hypothesis that dogs change their search strategy to adapt to changing meteorological conditions, by simultaneously measuring meteorological variables and dog behavior in open rangeland. We predicted that with higher temperature, lower humidity, and higher wind speed search dogs would be less accurate in following the experimental trail and would shift their sampling from airborne to the more stable substrate odors.

Materials and methods

Study animals

Six domestic dogs (*Canis lupus familiaris*) were used in this study (mean age 6 ± 1.67 years), 4 females (3 German Shepherds and 1 English Border Collie) and 2 males (German Shepherd and Labrador Retriever). All dogs were trained and certified mission-ready by the California Rescue Dog Association. The dogs specialize in trailing searches, where a dog searches the ground to detect and follow a unique scent trail left by a moving human subject hours or days earlier. The research was approved by the Animal Care and Use Committee of the University of California, Berkeley.

Field site and experimental trail

The field site was located in Briones Regional Park, Martinez, California. The chosen location had a maximum elevation change of 36 m to reduce topographical conditions as a confounding variable for odor dispersion and search behavior. An 800 m trail was established using a custom global positioning system (GPS) logger (Ultimate GPS Module - MTK3339 chipset and Adafruit Assembled Data Logging Shield). The GPS logged data at 5 Hz, and data were then averaged to find the location at a resolution of 1 Hz to reduce measurement error (Moen et al. 1997; Oderwald and Boucher 2003; Lewis et al. 2007). A visual examination of the mapped experimental trail compared with the known path showed that the averaging of GPS waypoints was highly accurate.

The experimental trail began at the edge of a parking lot and followed the edge of a tree line for 93 m, before traversing open fields for the remaining 707 m (Figure 1a). In selecting the trail, we avoided established trails and physically constrained areas to ensure the dogs were not navigating the trail because it was practical or the only possible direction to travel. To prevent the dogs from using visual cues, the human search subject for whom the dogs were searching was hidden from view behind tall shrubs and trees at the end of the trail (Figure 1a). To prevent interference with the next dog searching the trail, a wide berth was given between the experimental trail and the route returning to the starting location and staging area. Meteorological data were collected at 31 waypoints located 25 m apart along the trail, including the starting and ending locations (Figure 1b).

Behavioral measurements

Custom dog harnesses were equipped with a data logger connected to the GPS device and a tilt ball sensor (Adafruit.com) to detect spatial location and head position, respectively (Figure 2a). The tilt ball sensor was adapted to register a "head-up" position when the dogs walked with their heads aligned with their spine. When their head was lowered more than 20 degrees, the sensor registered a "head-down" position. A head-up position was interpreted as the ordinary and air-scenting posture, whereas the head-down position indicated a ground-scenting posture. Harnesses also included a custom microphone modeled after Brugarolas et al. (2016) to record respiration patterns of dogs; due to low recording quality, these data were not analyzed.

Meteorological measurements

Ambient meteorological conditions were recorded using portable weather stations (Davis Vantage Vue 6250) mounted on a tripod at a height of 1.8 m. A handheld console paired with the weather station showed the relative humidity, temperature (Celsius), wind speed (meters/second), wind direction, and barometric pressure (mmHg). Absolute humidity was calculated from relative humidity and temperature during analysis. We interpreted these meteorological conditions based on the conditions measured when the dogs searched the trail (searching condition) and the conditions at the time the trail was laid (set-up condition). We refer to the difference between the searching condition and the set-up condition as the condition change. We then calculated the average searching condition and average condition changes as quantities averaged across all 31 waypoints to describe the overall trail conditions for a specific search event conducted by a specific dog.

Procedure

Searches occurred during 3 times of day, morning (08:00–10:00), afternoon (13:00–15:00), and evening (18:00–20:00). The study took place between June and December of 2017. These 3 times of day were chosen to capture a range of meteorological conditions. The consistent climate of this location in the Bay Area of California allowed similar weather patterns to be captured for each search event occurring at the same time of day, despite study days occurring weeks to months apart.

One hour prior to the arrival of the search teams, a researcher acting as the target odor walked the experimental trail. The researcher walked at a normal pace (~1.1 ms) and did not try to conceal their scent. Upon completing the trail, they remained stationary at the end of the trail for the duration of the trials. Six different researchers laid the trail for the search teams. To ensure that dogs were orienting to a specific trail laid on a particular day, no dog searched for the same person twice.

Each dog and handler team searched the experimental trail 3 times, once at each time of day (morning, afternoon, and evening), and were tested on different days that were a minimum of 1 week apart. No more than 4 teams participated at the field site on a given day. One team searched the trail at a time, and the next team would not begin until the previous team found the target. The order in which teams searched the trail on a given day was counterbalanced to prevent ordering bias due to the presence of scent trails from other

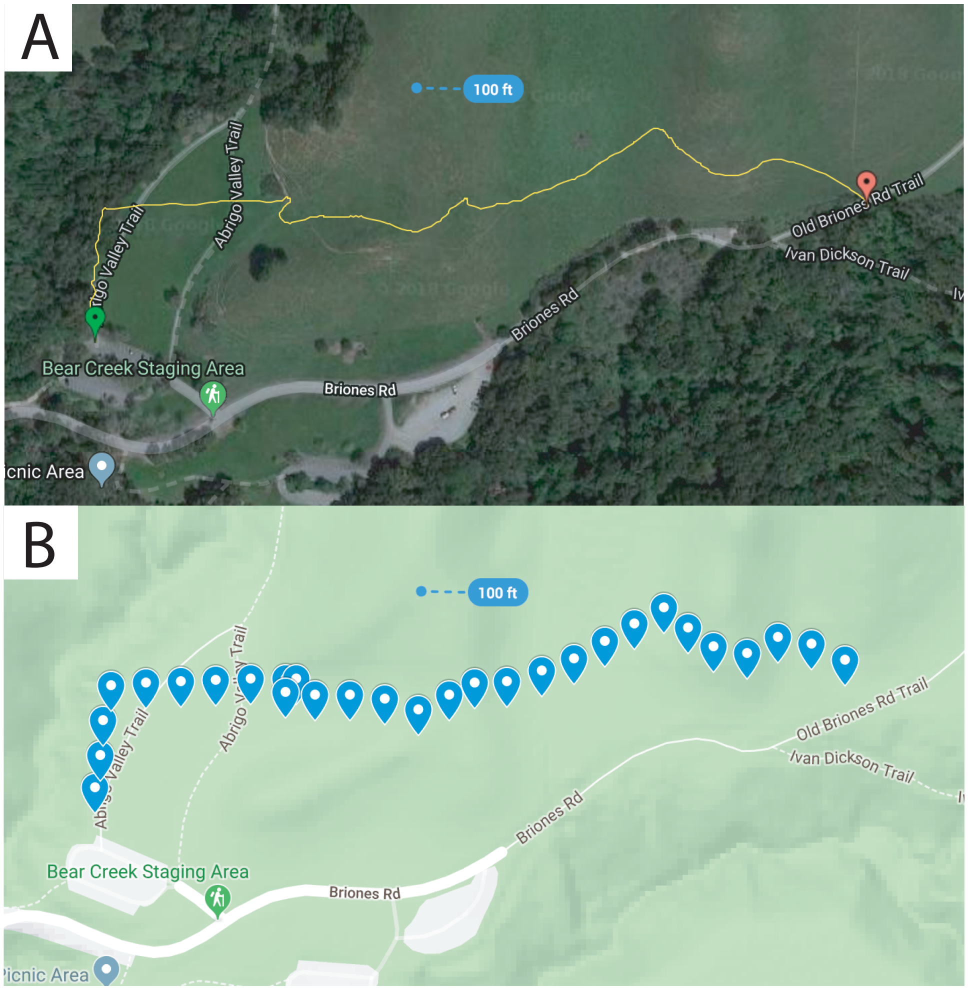

Figure 1. **(a)** Trail created by researchers acting as the "missing" person for the search teams to follow. All researchers walked the same direction from west to east. Green marker is the start of the trail, red is the end. **(b)** Thirty-one waypoints were marked 25 m apart on the trail, including the start and end point of the trail. The research team collected data about ambient weather conditions at each waypoint. The geography of the landscape is also shown in this panel.

search teams. We cued the dogs to the target person's scent using the standard protocol of the California Rescue Dog Association. A scent article was left by the target person at the start of the trail, such as an unwashed shirt or a sample taken by wiping the neck with a square cotton gauze. To reduce scent contamination (i.e., mixing of odors from different targets), the scent article was placed in a sealed plastic bag by the target. The search dog was then presented with the scent article by opening the plastic bag to expose the scented article. Dogs often required only a single short exposure to the scent article to complete the search. On one occasion, the scent was lost by the dog and the handler presented the scent article a second time.

At the start of a search event, researchers led the participating team to the start of the trail and initiated the data recording. We defined search event length as the time from the initial presentation of the scent article to the dog to the time the dog saw the target. Each handler was instructed to allow their dog to search naturally and handlers were not shown the trail map, to reduce the handler's biasing of their dog's search.

We collected meteorological data at 2 time points: immediately following the departure of the target (the set-up condition, used for the calculation of condition changes) and after the departure of each search team (the searching condition). A team of researchers followed the search team on the trail and recorded ambient temperature, humidity, barometric pressure, wind velocity, and wind speed at each of the 31 waypoints. Researchers waited 1 min at each waypoint before recording data to allow the weather station to stabilize and establish accurate local measurements. Data collection took ~30–40 min for the entire trail of 31 waypoints.

Analyses

Dog searching behavior was evaluated based on search posture (i.e., head-up or head-down) and location (relative to the experimental trail). The ratio of ground sampling to air sampling was quantified as the ratio of time spent in a head-down posture to time spent in a head-up position. To assess how closely dogs followed the human target's trail, we measured the area contained between the experimental trail and the dog's search path (Figure 3a). We also considered other common metrics used in trail-following experiments, including average distance from the trail and tortuosity. However, these proved less useful as brief but large excursions from the trail and circling behaviors erroneously indicated greater distances from the trail. In addition, we used a K–D tree algorithm to determine the distance and angle from the dog's location to the nearest waypoint, where the dog's position was determined from an average of every 10 consecutive GPS data points (Figure 3b).

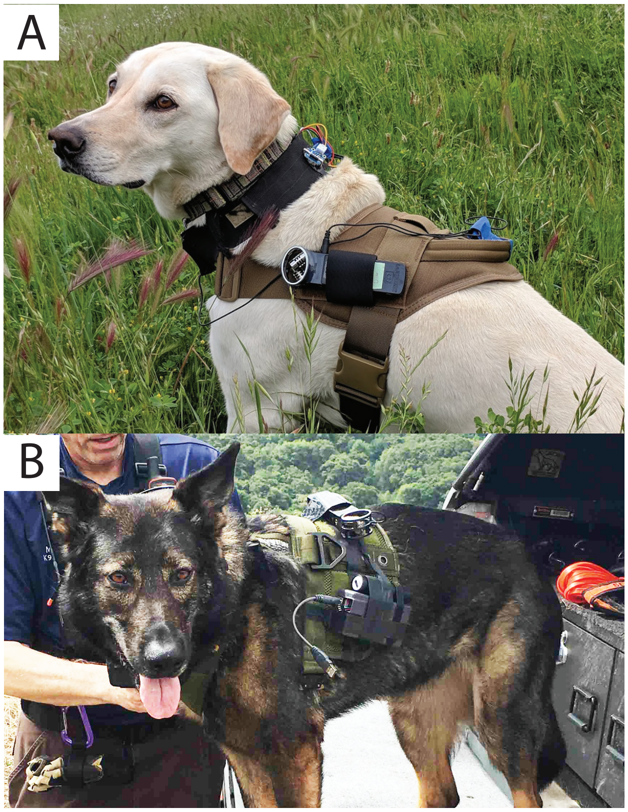

Figure 2. Search and rescue dog wearing research harnesses. **(a)** Audio recorder, microphone collar, and tilt switch (blue chip attached to collar) are shown. **(b)** Data logger for GPS and tilt switch.

We used linear mixed models (LMMs) and mixed effects logistic regressions to determine the search condition or condition change that had the largest influence on search behavior (R 3.5.1, *lme4* package). Dogs were included in each model as a random effect. In total, 10 metrics were included in each model: average searching conditions and average condition changes in wind speed, wind direction, barometric pressure, relative humidity, and absolute humidity. Variables were sequentially removed in a stepwise regression by removing nonsignificant variables with the highest *P*-value until only significant variables predicting the outcome remained. Conditional r^2 values are reported using the R *MuMIn* package for linear mixed effects models. Alpha was set to 0.05. Averages and standard deviations are reported throughout the text.

Results

Four of the 6 dogs completed search events at all 3 experimental times of day. The remaining teams completed one search event each, an evening and an afternoon search event. In total, 15 searches were performed with a 93% success rate of finding the human target. Dogs predominately stayed within 10 m of the experimental trail (Figure 4), suggesting that the bulk of the target's odor was concentrated within that distance of that trail. Search teams averaged 14.23 ± 4.34 minutes to locate the target. Dogs searched at an average speed of 0.89 ± 0.82 ms, with some dogs averaging higher speeds, up to 1.6 ms. Overall, dogs traversed 981.7 ± 161 m in comparison to the 800 m long trail laid by the person. The average area of the between-trails region was 5373.0 ± 2378.32 m^2.

Figure 5a shows an example of an individual dog's search, as defined by their trajectory and head positions, and in relation to the experimental trail, with corresponding wind conditions. Figure 5b shows the 15 search trajectories for all dogs. The observed inter-individual variability in the search paths leading to the target indicated a dog was navigating from cues based on the target's scent rather than scent contamination or trail memory. The paths taken by the dogs were remarkably consistent across search events, although during two searches, the same dog strayed far from the trail before recovering the odor and returning to the correct trajectory (Figure 5b). A small hill was present in the last quarter of the trail. The dogs often searched below the main trail, which suggests that odors were dispersing down the slope. When farther from the experimental trail, dogs were observed making loops before returning to the main trail. Finally, dogs did not appear to use visual search to detect targets, even when close to the human target sitting on the ground in an unobstructed view at the end of the trail. They continued to put their heads down to sniff the ground during this time. Thus, it appears that the dog's use of the head up position primarily functioned for sampling airborne odors and not for scanning the landscape visually. This is consistent with a study of the relative use of olfactory and visual cues by sniffer dogs searching for explosives under dim and bright light conditions, in indoor and outdoor settings (Gazit and Terkel 2003a). Dogs were equally accurate under both light conditions, whether indoors or outdoors. While the dogs panted more heavily when searching outdoors in the bright light condition, there was no evidence that dogs used vision to orient to the location of the familiar explosive containers, either the targets or the dummies, which were clearly visible. This suggests that in our study the dog's raised head position functioned primarily to collect olfactory information.

Meteorological conditions

In total, 434 meteorological data points were collected. Average searching conditions were compared across the different experimental times of day in Table 1. Morning conditions and evening conditions were similar, though mornings were drier and windier than evenings. Afternoon conditions were especially hot and dry. Correlations were calculated between temperature, relative humidity, absolute humidity, barometric pressure, and wind speed. A strong correlation was found between temperature and relative humidity (r = −0.86) as well as temperature and absolute humidity (r = 0.82). Therefore, temperature was excluded from the LMMs to avoid multicollinearity.

Table 1 also shows how the difference between conditions at set-up and during search varied with time of day. During morning search events, humidity decreased across the condition change interval, that is, from the time that the trail was laid to the time that the trail was searched by dogs. The reverse occurred in evening search events: temperature decreased and humidity increased between the set-up of the trail and the search of the trail by dogs.

Potential design effects

Each search event executed by the same dog was separated by an average of 9.63 ± 3.96 days. Analysis by LMM revealed that the number of searches each dog had previously performed had no effect on the time needed to complete a search (14.23 ± 4.34 min; β = −48.06, $t_{8.4}$ = −0.79, P = 0.45; cond. r^2 = 0.21, Table 2). In addition, the number of previous searches had no effect on the calculated area between trails (6919.10 ± 2378.33 m^2; β = −826.02,

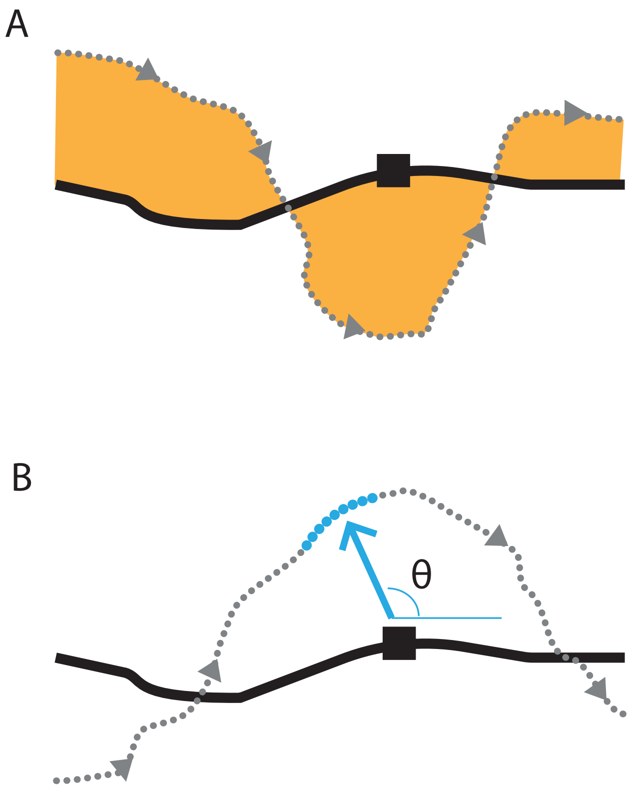

Figure 3. A schematic representing the 2 metrics used to assess how closely to the person's trail a dog was during the trials. Example dog trail shown in dotted gray line, example person's trail in black. A waypoint is represented by a black square. **(a)** The between-trails area was calculated by finding the area of the region (orange) between the dog's trail and the person's trail. **(b)** The distance and angle from weather station waypoint to the dog was found by averaging the 10 closest points on the dog's trail to the weather station.

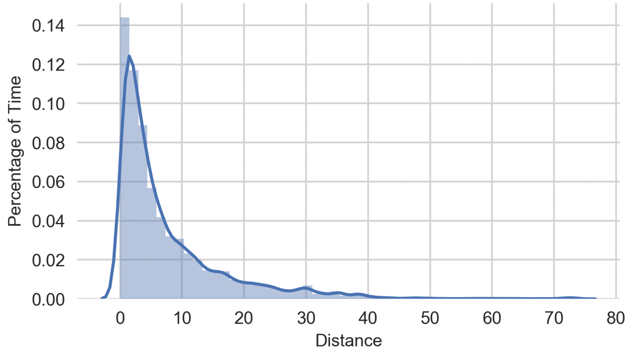

Figure 4. Distribution of distances from the person's trail, all dogs for all searches. The majority of the time dogs are within 10 m of the person's trail.

$t_{8.9} = -1.12$, $P = 0.29$; cond. $r^2 = 0.22$, Table 2). Finally, repeated searches on the same trail did not improve performance.

It is possible that a dog could have followed the scent of the previous search team. To compensate, the starting order of dogs for days with multiple search teams on site was counterbalanced such that no search team was the first to search more than once. LMM results revealed that starting order had no effect on time ($\beta = -35.06$, $t_{8.8} = -0.61$, $P = 0.56$; cond. $r^2 = 0.53$, Table 2) or between-trail area ($\beta = 6.36$, $t_{10.5} = 0.01$, $P = 0.99$; cond. $r^2 = 0.11$, Table 2). Hence, start order had no effect on search performance.

Environmental conditions affect odor dispersion from trails

A backwards stepwise regression revealed that average relative humidity during the searching conditions remained as the factor which had the greatest effect on the distance of a dog's chosen path to the experimental trail (Figure 6, $\beta = -90.08$, $t_{10.4} = -3.4$, $P = <0.01$, cond. $r^2 = 0.50$, Table 2). The higher the relative humidity, the closer dogs searched to the experimental trail. Each percent increase in relative humidity, on average, led to a reduction of ~90 m^2 in the between-trails area. This suggests that current conditions during the time of a search may be more important for olfactory orientation than any changes in conditions that may have affected the odor between the deposition and search.

We also investigated the effects of small-scale meteorological variations along the trail and their effects on odor dispersion. An LMM was implemented to determine relationships between the 31 individual waypoint readings and a dog's average distance to that waypoint. Among the meteorological conditions measured at each waypoint, higher relative humidity during the search resulted in dogs searching closer to the person's trail ($\beta = -0.10$, $t_{284.6} = -4.96$, $P = <0.01$; cond. $r^2 = 0.11$, Table 2). In addition, higher wind speed resulted in dogs searching farther away ($\beta = 0.65$, $t_{418.8} = 2.69$, $P = <0.01$, cond. $r^2 = 0.11$, Table 2). Meteorological condition changes between setting up the trail and searching the trail had no effect on a dog's search distance from each waypoint. A final LMM revealed that wind direction had no impact on the dog's location relative to the waypoint ($\beta = 0.6534$, $t_{352.8} = 2.69$, $P = 0.21$, cond. $r^2 = 0.04$, Table 2).

Sampling behavior

Dogs spent ~16.7 ± 13.1% of search time sampling the ground, that is, in a head-down position. A mixed-effects logistic regression model revealed that the faster a dog was moving, the lower the odds that it was sampling the ground ($\beta = -0.25$, $z = -6.73$, $P < 0.01$, Table 3). For every increase of 1 ms in speed, the odds of a dog sampling the ground dropped by 22%. A second mixed-effects logistic regression showed a marginal, not significant, relationship between distance from the trail and the odds of ground sampling ($\beta = -0.004$, $z = -1.73$, $P = 0.08$, Table 3). This effect was low, with only a decrease of 1% in odds of air-sampling for each meter away from the person's trail that a dog traveled. These 2 findings suggest that search dogs trained to trail humans prefer to sample the air rather than the ground.

As a dog moved away from the experimental trail, it adjusted its speed according to its distance from the trail (Figure 7). Within the first 40 m, dog speed increased, then decreased following a quadratic pattern (Table 2). Beyond 40 m, dog speed linearly increased with distance from the trail (Table 2). The frequency of dog ground sampling (color coding for symbols in Figure 7) similarly transitions from relatively low values to higher values at a distance of ~40 m from the trail. Taken together, these patterns indicate dog behavior exhibits distinct regimes depending on distance from the trail. Within a threshold distance from the trail, dogs follow the odor with an air-sampling strategy. Farther from the trail, dogs move with increasing speed and are more likely to employ a ground-sampling strategy. An intermediate region between 20 and 30 m away from the trail indicates transitional behavior, where dogs slowed their speed while still predominantly sampling from the air rather than the ground.

Discussion

Our study addressed how trained search dogs oriented to olfactory trails in a natural landscape subject to transportation and phase

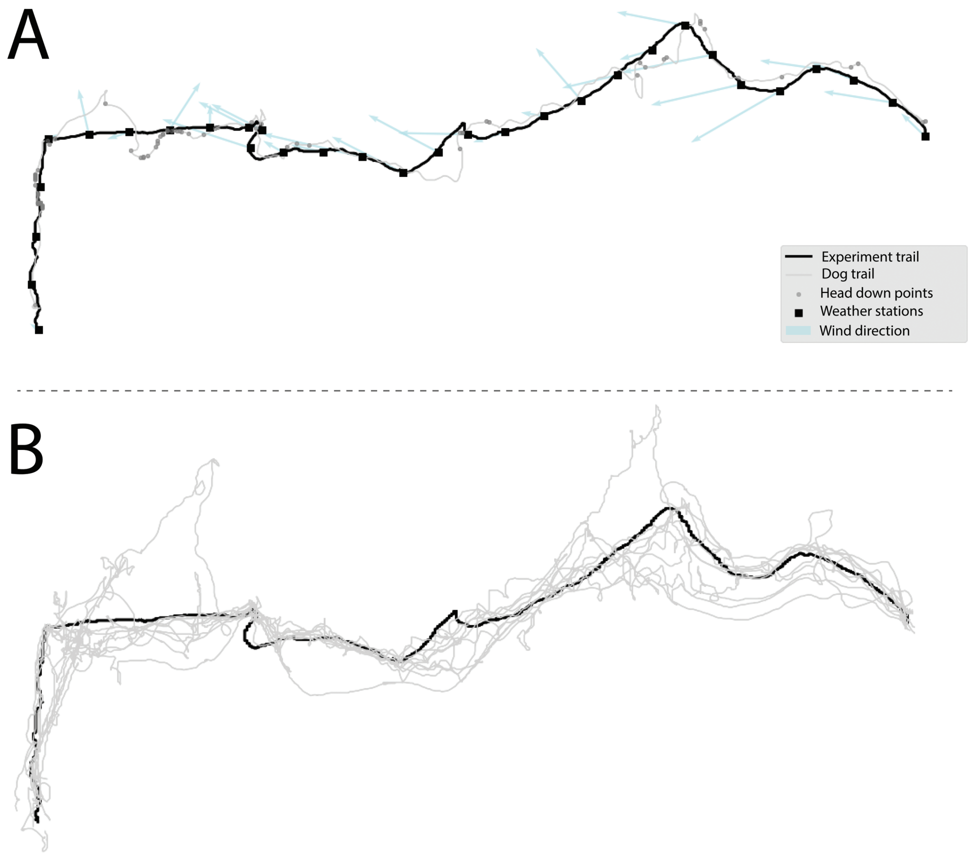

Figure 5. Two different overhead views of the target person's trail and dogs' trails. **(a)** An example of a search performed by a team. Trails ran from west to east. Black line shows the experimental trail walked by the target person. Black squares show the location of each waypoint where meteorological data were recorded both before and during the dogs' searches. Light gray line is the dog's path. Gray circles on the line show whenever a dog sampled odors from the ground. Blue vectors show relative wind speed and direction. **(b)** All 15 search paths taken by dogs during the study.

Table 1. Average meteorological conditions for each period of the day when searches took place

	Prevailing conditions during search					
	Temperature (°C)	Relative humidity (%)	Absolute humidity (%)	Barometric pressure (mmHg)	Wind speed (m/s)	Wind direction (degrees)
Morning	16.77 ± 0.86	61.11 ± 10.18	8.70 ± 1.31	742.55 ± 2.36	2.51 ± 1.55	184.81 ± 79.29
Afternoon	30.96 ± 5.82	41.79 ± 11.70	12.89 ± 1.16	756.39 ± 6.70	1.81 ± 0.96	153.13 ± 107.2
Evening	16.60 ± 6.85	74.92 ± 8.62	10.89 ± 3.05	751.46 ± 5.75	0.97 ± 1.12	189.07 ± 90.55
	Temporal changes between trail laying and search					
	Temperature (°C)	Relative humidity (%)	Absolute humidity (%)	Barometric pressure (mmHg)	Wind speed (m/s)	Wind direction (degrees)
Morning	2.01 ± 0.83	−5.48 ± 4.20	0.33 ± 0.48	0.44 ± 0.92	0.73 ± 1.25	−18.19 ± 104.16
Afternoon	1.14 ± 1.08	−2.12 ± 2.54	0.02 ± 0.55	-0.57 ± 0.38	0.38 ± 1.11	38.63 ± 108.25
Evening	−4.35 ± 1.48	13.53 ± 4.48	−0.51 ± 0.35	3.32 ± 6.11	−0.63 ± 1.04	−57.75 ± 104.17

shifts due to changes in meteorological conditions. Trained search dogs maintained a high level of success, despite changes in relative humidity and air temperature, adjusting their strategy with the demands of the environment. The degree of spatial search deflection from the original trail was significantly greater when the air was hot and dry, even though overall search success was high across all weather conditions. Under hot and dry conditions, dogs moved more slowly and sampling odors on the ground; when temperatures were lower and humidity was higher, they moved rapidly while sampling air-borne odors. Dogs alternated between these two strategies dynamically according to their distance from the trail. The overall success rates found in the present study (93% on average) is similar to that found in earlier studies (from 65% to 82%: Greatbatch et al. 2015; Woidtke et al. 2018). We extended this earlier work by further demonstrating a correlation between this high success rate and the dog's search strategy under different

Table 2. Linear mixed effects model results

Model		β	Std. error	df	*t*	*P*
Time (s) to complete search predicted by previous number of searches	Intercept	938.08	148.07	12.0	6.34	<0.001*
	Search number	−48.0	61.18	8.42	−0.79	0.45
						cond. r^2 = 0.55
Between trails area (m²) predicted by previous number of searches	Intercept	6919.10	1584.98	10.985	4.37	0.001*
	Search number	−826.02	739.5	8.89	−1.12	0.29
						cond. r^2 = 0.22
Time (s) to complete search predicted by starting order	Intercept	896.49	122.1	10.8	4.34	<0.001*
	Start order	−35.06	57.6	8.77	−0.61	0.56
						cond. r^2 = 0.53
Between trails area (m²) to complete search predicted by starting order	Intercept	5340.13	1236.59	11.93	4.32	0.001*
	Start order	6.36	708.61	1.45	0.01	0.99
						cond. r^2 = 0.11
Between trails area (m²) predicted by average search conditions(result of backwards stepwise regression)	Intercept	10 711.98	1657.52	11.69	11.69	<0.001*
	Relative Humidity	−90.08	26.52	10.34	−3.40	<0.01*
						cond. r^2 = 0.50
Dog distance (m) to each waypoint predicted by search condition at waypoint	Intercept	12.90	1.39	124.16	9.29	<0.001*
	Relative humidity	−0.10	0.2	284.56	-4.96	<0.001*
	Wind speed	0.65	0.24	418.82	2.69	< 0.01*
						cond. r^2 = 0.11
Angle (degree) of dog's location to way point as predicted by wind direction (degrees from North)	Intercept	189.41	10.89	11.85	17.39	<0.001*
	Wind direction	0.07	0.05	352.78	1.26	0.21
						cond. r^2 = 0.44
Speed predicted by distance from the experimental trail for distances <40 m	Intercept	0.95	0.19	5.02	4.92	< 0.01*
	Distance (m)	0.03	0.002	14 982.00	13.67	< 0.001*
	Distance²	0.001	< 0.001	14 981.33	−13.97	<0.001*
						cond. r^2 = 0.33
Speed predicted by distance from the experimental trail for distances >40 m	Intercept	2.21	0.55	5.40	4.00	<0.01*
	Distance (m)	−0.02	0.01	143.86	−3.62	<0.001*
						cond. r^2 = 0.59
Ground sampling behavior predicted by average search conditions (result of backwards stepwise regression)	Intercept	0.76		5.23	12.42	<0.01*
	Wind speed (m/s)	0.02		430.18	2.19	0.03*
						cond. r^2 = 0.35

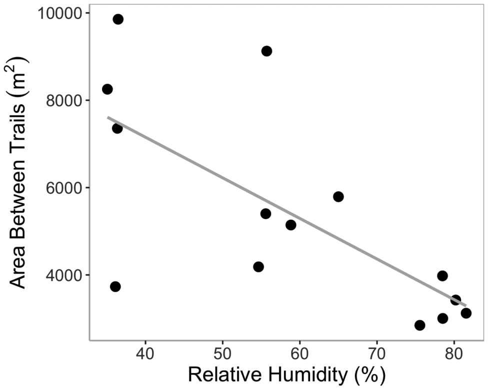

Figure 6. Relationship between relative humidity and the area between trails. Odor disperses less in high humidity and dogs are able to follow closer to a person's scent trail.

meteorological conditions. Our study thus quantified a phenomenon well known to search and rescue teams: that an expert search dog dynamically changes its search strategy in response to shifts in ambient weather conditions.

Influence of atmospheric conditions

Of the 10 meteorological variables measured, the variables with the largest effects on search behavior were relative humidity and, by implication due to high correlation, air temperature. On cooler, more humid days, the dogs searched closer to the original trail, possibly because the trail odors spread less widely. This is also observed in other contexts and species: in cooler temperatures, gypsy moths track a narrower plume, flying with tighter turns, and a more direct flight to the odor source (Charlton et al. 1993). In humans, decreased air temperature is correlated with lower detection of malodors (Guo et al. 2005; Dalton et al. 2011; Afful et al. 2016).

The distance searched from the original trail could simply represent the wider odor plumes found in turbulent, hot air. Because of the decay of mean concentration and concentration fluctuations, such plumes would be more dilute and homogeneous in concentration (Deardorff and Willis 1984; Fackrell and Robins 1982; Wilson et al. 1985). Dogs would then have to increase their distance to locate the odor plume edge to successfully follow the scent. This would be functionally akin to casting, where search trajectories are made orthogonal to the plume gradient. Casting is found in diverse animal species and spatial scales, from walking insects to flying birds (Kuenen and Cardé 1994; Zimmer-Faust et al. 1995; Vickers 2000;

Table 3. Mixed effects logistic regression results

		β	Std. error	*z*	*P*
Probability of sampling the ground predicted by speed of dog's movement	Intercept	−1.28	0.41	−3.11	<0.001*
	Speed (m/s)	−0.25	−6.68	−6.73	<0.01*
Probability of sampling the ground predicted by distance from the experimental trail	Intercept	−1.49	0.42	−3.53	<0.001*
	Distance (m)	−0.004	0.002	−1.73	0.08

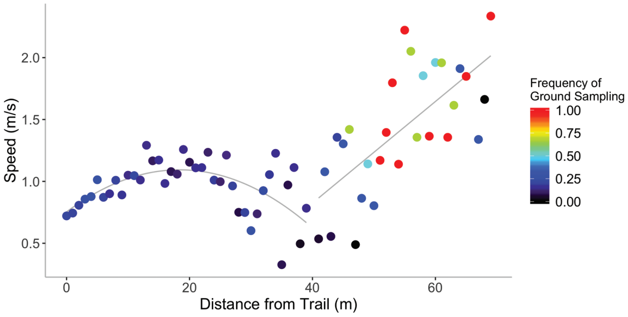

Figure 7. Relationship between movement speed, distance from the trail, and ground sampling frequency. Dogs appeared to display 2 distinct behaviors depending on their distance from the trail. Within 40 m, dogs display a quadratic relationship between distance, travel speed, and frequency of ground sampling. Beyond 40 m, dogs appear to have lost the odor trail and begin to increase their speed linearly as well their frequency of ground sampling.

Willis 2005; Gagliardo 2013), as it identifies the plume boundaries and allows the navigator to relocate the directional gradient (Finelli 1999; Finelli et al. 2000).

The human trail odors could have been present in 1 or more physical phases depending on the temperature and humidity. The combined effects of temperature and humidity lead to complicated dynamics in the phase, concentration, and distribution of organic molecules. These effects are further dependent on the size and hydrophobicity of the molecule in question, and the availability of substrate binding sites (Seinfeld and Pandis 2016). As humidity increases, substrate moisture content also increases. This could cause odor molecules that were previously bound to the substrate to enter the vapor phase, as water molecules begin to out-compete odor molecules for sorption sites in the soil (Spencer and Cliath 1970; Unger et al. 1996). For example, yellow pine chipmunks use olfaction more successfully to detect buried seed caches when air and soil are more humid (Vander Wall 2003). Similarly, dogs may have searched more accurately during high relative humidity conditions because odorant components desorbed from the soil and became more available for olfaction close to the trail.

Wind also affects the movement of odors. Increased wind speed can increase both chemical and pressure vertical gradients, which in turn enhances the rate of volatilization of organics (Farmer et al. 1972). Once an odor is airborne, either in the vapor or aerosol phase, its spatiotemporal distribution is dictated by the flow physics of the local atmosphere. During the afternoon, when air temperature increased by an average of 14 °C from the morning, there would be both increased vapor pressure, increasing odor transition into the vapor phase, and greater turbulence, favoring upward transport into higher atmosphere elevations (Baldocchi et al. 1988). Wind also extracts and mixes volatilized substances (Kimball and Lemon 1971). All these processes would theoretically decrease odor perception (Xing et al. 2007) and explain why under hot, dry conditions, or under conditions of increased wind speed, the dogs searched farther from the experimental trail.

Because we measured ambient conditions before and after the search, we were able to distinguish the effects of the immediate weather conditions. There was a significantly larger effect of meteorological variables measured during the search condition than the set-up condition. This suggests that the age of a trail is a pertinent variable which should be explored in future studies.

Search and sample strategies

Dogs moved most quickly when sampling air within 10–20 m of the trail. When 20–40 m from the trail, dogs reduced speed and increased ground sampling. Beyond 40 m, dogs increased both speed and ground sampling. They also moved rapidly in circles and loops, searching ground odors (Figure 5). Interviews with the handlers revealed that they interpret this behavior as a signal that the dog has lost the main odor trail. The dogs gradually expanded the diameter of the loops, searching back and forth for some time before they continued in a straight trajectory, indicating that they re-located the odor. This distance threshold has also been observed in dogs searching for endangered desert tortoises; they appear to lose the odor 20–40 m from the tortoises' locations (Cablk et al. 2008). Air very near the ground surface resides in a boundary layer which likely retains more odors (Moore et al. 1994), and hence ground sampling is a more sensitive sampling method. Thus, having lost the odor, dogs appear to cast and direct their efforts to the air near the substrate where odors are often more accessible.

Dogs also used ground sampling when they were moving slowly and <10 m from the trail. This may represent a solution to a different search problem; instead of searching for a lost plume, here a dog may be seeking different kinds of information from the location with the highest odor concentration. For example, the dog might have been detecting multiple human scents and had returned to the trail to relearn the target odor, which would be the freshest odor on the trail. Human body odor is a complex stimulus (Natsch et al. 2020). A search dog can quickly discriminate the direction of human movement, discriminating human footsteps that have been deposited only seconds apart (Thesen et al. 1993). Thus, search dogs can determine the direction of travel from no more than 5 human footsteps (Hepper and Wells 2005).

There are also physiological constraints that can influence olfactory search. For example, there is evidence from humans that olfactory detection thresholds decrease in more humid air. (Kuehn et al. 2008). This response could also be true in dogs and should be addressed in future studies. Second, the dog may experience a conflict between respiration for temperature control and respiration for olfactory samples, as dogs pant to reduce body temperature after physical exertion and/or in hot ambient conditions (Crawford 1962). A dog closes its mouth to sniff and therefore cannot control temperature by panting at the same time (Rosell et al. 2018). Thus, an increased need for cooling must reduce the quality and quantity of odor sampling (Steen et al. 1996; Gazit and Terkel 2003b; Settles et al. 2003). Under hot conditions, therefore, the dogs could have had less information from olfactory sampling about plume location, leading them to lose the trail and hence widening their search area in an effort to relocate the plume.

Finally, there were significant individual differences in search strategy, with each individual dog showing different frequencies of air and ground sampling. For example, the English Border Collie spent a greater proportion of search time using ground sampling than the other dogs and also moved at a slower pace, yet was as successful as the others, all either German Shepherds or Labrador Retrievers. Thus, it is possible that future research could uncover predispositions at the level of breed or training history on search strategy under different environmental challenges. The use of the search dog as an experimental paradigm suggests a host of fundamental questions about cognitive processes under natural conditions, from stimulus perception to decision making, all of which must be involved during olfactory navigation.

The domestic dog makes a unique and critical contribution to society, in search and rescue, conservation biology, medical diagnosis, and law enforcement (Rosell 2018). Search dogs are thus emerging as an experimental paradigm, important both for their invaluable contributions to society and advancing theoretical questions in behavior and cognition. Despite the emergent field of dog cognitive psychology (Horowitz 2014), there is a remarkable paucity of studies on the cognition underlying olfactory search in dogs. The present study demonstrated that small changes in ambient meteorological conditions can shape the search strategy of a large mammal orienting to an odor trail. Our results complement past work on search dog behavior and extend the current work on the neural mechanisms of olfactory trail following in laboratory rodents (Baker et al. 2018). This work also provides support for future studies on the cognitive challenges faced by olfactory navigators while flexibly adapting search strategy to the unpredictable statistics of an odor plume under natural conditions.

Conflict of interests

None declared.

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