Something in the wind: The influence of wind speed and direction on African lion movement behaviour

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Data Availability Statement

Analyses reported in this article can be reproduced using the data provided by Wijers et al. (2022).

Abstract

Olfaction is a key sense, enabling animals to locate forage, select mates, navigate their environment, and avoid predation. Wind is an important abiotic factor that modulates the strength of olfactory information detected by animals. In theory, when airflow is unidirectional, an animal can increase odour detection probability and maximise the amount of olfactory information gained by moving crosswind. Given energetic costs inherent to activity and locomotion, behavioural search strategies that optimize the benefit-cost ratio should be advantageous. We tested whether African lions (*Panthera leo*) modify their movement directionality and distance according to wind speed and direction during hours of darkness when they are most active. We tracked 29 lions in southern Zimbabwe using GPS collars and deployed a weather station to collect detailed abiotic data. We found that when wind speeds increased lions were more likely to move crosswind. We also found that female lions, which tend to hunt more often than males, travelled farther when wind speeds were stronger. The results of our analysis suggest that lions adjust their movement behaviour according to wind speed and direction. We inferred that this was a behavioural decision to maximise the amount of olfactory information gained per unit of energy spent. Our findings not only offer one of the first detailed insights on large carnivore anemotaxis (movement direction relative to wind) but also make an important contribution towards understanding the influence of wind on predator ecology in general which remains understudied to date.

Running head

Wind influences lion movement behaviour

Keywords

Panthera leo, anemotaxis, wind, movement behaviour, olfaction

Introduction

The behavioural decisions of animals are shaped by intrinsic individual characteristics in combination with prevailing biotic and abiotic conditions in the environment (Manning and Dawkins, 1998). Animals will respond to a range of biotic conditions including food availability, interspecies interactions and the presence or absence of mates (Dobson 1982; Hof et al. 2012). Additionally, abiotic conditions such as precipitation, light, lunar phase, and temperature, can influence organismal functioning and modulate the relative costs and benefits associated with particular activities (Wolfe and Tan Summerlin 1989; Stokes et al. 2001; Lopes and Bicca-Marques 2017). Changes in these environmental conditions can therefore induce behavioural changes where the choice of behaviour is generally expected to maximise the individual’s probability of survival and reproductive success (Mcfarland 1977).

Movement is a fundamental behaviour exhibited by most animals and is essential for nutritional recruitment, locating conspecifics for reproduction, and minimizing threats to survival (Bernstein 2001). However, movement decisions also carry energetic costs that are expected to be optimised enabling animals to accrue maximum benefit while minimizing expenditures (Tucker 1975; Chassin et al. 1976; Halsey 2016). To this end, animals have evolved various behavioural strategies in response to changes in abiotic conditions. Behavioural strategies include, for example, restricting movement to periods with comparatively favourable environmental conditions or altering movement speed, tortuosity, and direction (Stelzner 1988; Oosthuizen and Bennett 2015; Thaker et al. 2019). Several classes of animals have also been found to dynamically adjust their movement direction according to wind direction; behaviour known as anemotaxis. This behaviour has been observed among gastropods (Kalmus 1942; Farkas & Shorey 1976), insects (Kennedy and

Marsh 1974; Johnston 1982), birds (Nevitt et al. 2008), and mammals (Schooley and Branch 2005; Togunov et al. 2017). The type of anemotaxis, whether that be upwind, downwind or crosswind orientation, varies according to species' physiology and ecology (Farkas and Shorey 1976; Togunov et al. 2017). Although anemotaxis can be employed for a variety of reasons (e.g. for navigation, thermoregulation, or to reduce desiccation), one of the main purposes is to improve olfactory search efficiency (Sabelis & Schippers 1984).

Olfaction is a key sensory attribute that many animals use when making foraging, communication or predator avoidance decisions and is modulated by wind (Sündermann et al. 2008; Ruzicka and Conover 2011). Wind disperses odour molecules from their source in a smoke-like plume that extends and expands according the direction and strength of airflow (Murlis et al. 1992). All animals give off olfactory cues either as a result of involuntary metabolic processes or through the deliberate production of chemicals expressed from specialised scent glands (Banks et al. 2014). These olfactory cues are then detectable more broadly which can facilitate the exchange of inter- and intra-specific information. Such information is particularly consequential among the interactions of predators and prey. These interactions are loosely described by an arms race whereby predators use all available information to optimise the search for prey and prey do the same in avoiding being killed (Dawkins and Krebs 1979). Chemical cues also facilitate communication between conspecifics and play a significant role in mate location and selection in many mammalian species (Charpentier et al. 2010; Baum 2012). Animals searching for prey or conspecifics using olfactory cues might be expected to account for wind direction and to adjust their movements accordingly to optimise their search behaviour (Pyke 1984).

Theoretically, the probability of detecting odour cues is maximised when moving crosswind, as illustrated by Sabelis and Schippers (1984). This is because the size of the area inspected per unit distance travelled is greater than it would be if moving upwind or downwind (provided that the variation in wind direction is less than 30 degrees from the mean). An animal moving directly into the wind would only be able to detect odours originating from the narrow air column ahead of it while the size of the search area created by crosswind movement would be approximately equivalent to the detection distance from the source multiplied by the distance travelled. Evidence of crosswind movement has recently been reported for adult female polar bears (*Ursus maritimus*) which appear to adopt this behavioural strategy most frequently on winter nights, when hunting behaviour is likely (Togunov et al. 2017). However, apart from this study, and the familiarity of naturalists to wind direction influencing mammal behaviour, research investigating crosswind search behaviour among terrestrial predators remains sparse.

African lions (*Panthera leo*), like many other felids (Macdonald 1985), rely on olfactory cues for a number of their life history strategies (Gilfillan et al. 2017). Both males and females scent mark through urination and possibly also via secretions from pedal glands when paw scraping to communicate with conspecifics (Kleiman and Eisenberg 1973; Gilfillan et al. 2017). Behavioural and chemical analyses have established that urine scent marks enable receiving lions to acquire information on the sex and social affiliation of the signaller (Andersen and Vulpius 1999; Gilfillan et al. 2017). While olfaction is known to be an important sensory component of lion communication, the degree to which lions depend on scent detection to locate prey is not well understood. Some studies have suggested that felids rely primarily on visual and auditory cues, and olfactory cues secondarily, when hunting prey (Kleiman and Eisenberg 1973; Ferreira and Funston 2010; van Valkenburgh et al. 2014). This assumption is consistent with the stalk-and-ambush hunting technique that lions employ most frequently (Hopcraft et al. 2005) rather than the cursorial method used by predators, such as canids, which are more reliant on olfactory cues (van Valkenburgh et al. 2014). However, as described by Elliott et al. (1977), lion prey capture can consist of several phases: search, stalk, attack, and subdue. The search phase is defined as “the reduction of predator – prey distance for prey which has not been specifically located” (Elliott et al. 1977; p. 1813). While not all hunts involve the search component, exploiting olfactory information to locate prey and reduce search time would have clear advantages. Furthermore, lions are known to acquire a significant proportion of their nutritional requirements by scavenging (Hopcraft et al. 2005). To locate carcasses, lions are likely to be more dependent on auditory (e.g. following feeding vocalisations from other scavengers) and olfactory stimuli.

Although no studies have specifically investigated the role of olfactory search behaviour in lion prey acquisition, wind has been found to correlate with lion hunting success (Stander and Albon 1993; Davies et al. 2016). Lion kills in South Africa’s Addo Elephant National Park and Namibia’s Etosha National Park were found to occur more frequently during periods with higher wind speeds (Stander and Albon 1993; Davies et al. 2016). This pattern was attributed to the increased noise associated with high winds resulting in reduced auditory detection of lions by prey (Leuthold, 1977). Additionally, lions in Etosha apparently stalk prey by moving upwind or crosswind more often than downwind and are more successful in doing so (Stander 1992). This finding somewhat contradicts results reported by Elliott et al. (1977) which showed that lions in Ngorogoro Crater, Tanzania, did not appear to consider wind direction when stalking prey, though approaches were slightly more common in crosswind directions. Stalk behaviour, however, represents a small fraction of the overall distance travelled by lions and only occurs once prey have been visually detected (Elliott et al. 1977). In such cases, movement relative to wind is probably aimed at reducing olfactory detection by prey rather than maximising detection of prey. Nevertheless, the ways in which lions respond to wind during other periods of locomotion, such as the search phase described by Elliott et al. (1977) or when searching for olfactory information on conspecifics, remain unclear. Here, we attempted to resolve this question by GPS-tracking 29 lions in southern

Zimbabwe. Given the importance of olfaction for communication and the potential benefits of using olfactory cues when searching for prey, we predicted that lions would; *i*) be more likely to move crosswind to maximise search success and *ii*) travel farther in higher winds to take advantage of the greater search efficiency that is possible in such conditions (*sensu* Elliott et al. 1977). However, as most lion hunting attempts occur nocturnally, search behaviour has also been found to be modulated by moon light (Elliott et al. 1977). Specifically, lion hunting success increases during darker periods when the moon is below the horizon or just new (Van Orsdol 1984; Funston et al. 2001b; Packer et al. 2011; Davies et al. 2016). Thus, we considered lunar cycle when assessing the nature and strength of wind effects on lion movement behaviour.

Methods

Study site

We positioned this study in Bubye Valley Conservancy (BVC), a 3400 km^2 privately-owned wildlife reserve in southern Zimbabwe (Fig. 1). The BVC hosts a large lion population (ca. 500 individuals; du Preez et al. 2015) along with a several sympatric large carnivore species including brown hyaenas (*Hyaena brunnea*), spotted hyaenas (*Crocuta crocuta*), leopards (*Panthera pardus*), and cheetahs (*Acinonyx jubatus*). The diverse large carnivore guild is supported by a variety of prey species including zebra (*Equus quagga burchellii*), wildebeest (*Connochaetes taurinus*), eland (*Taurotragus oryx*), buffalo (*Syncerus caffer*) and kudu (*Tragelaphus strepsiceros*). Vegetation across the conservancy is primarily mopane (*Colophospermum mopane*) woodland savanna with riparian woodland occurring along ephemeral streams. Typical climatic conditions in the region consist of high daytime temperatures (>40°C) and relatively low rainfall (~ 351 mm) in the summer months (e.g., November to March) with milder and dryer conditions across the remainder of the year. Winds tends to blow from the southeast for most of the year with a shift towards the northeast in June and July (Fig. S1). Wind speeds are generally lower in the first half of the year and increase above the annual average in spring (October – November).

Data collection

Between February and December 2014, we tracked 29 GPS-collared lions (14 females and 15 males; Table S1) in BVC. We programmed the collars (Africa Wildlife Tracking, Pretoria, South Africa) to record 16 geographical locations per day with an hourly interval between 1700 and 0700 local time and one point at 1400. Each lion was chemically immobilized using 75-100 mg Zoletil (Virbac RSA (Pty) Ltd, Halfway House, South Africa) combined with 5 mg medetomidine (Kyron Laboratories, Johannesburg, South Africa). Immobilization drugs were delivered intramuscularly by 1 cc darts (Pneudart, Williamsport, PA, U.S.A.) projected from a Dan-Inject CO2-pressurized dartgun (Dan-Inject, Børkop, Denmark) at approximately 20 m from the animal. Approximately 15 minutes after injection, the animal was carefully blindfolded and earplugs inserted to reduce visual and auditory disturbance. We then fit the collar around the neck. At 60 minutes after initial drug injection, 25 mg atipamazol (Antisedan, Pfizer Animal Health, Johannesburg, South Africa) was administered intramuscularly by hand to reverse the effects of medetomidine enabling the animal to recover mobility within 15 – 90 minutes. All capture and handling protocols were carried out in accordance with the recommendations of the ASAB/ABS Guidelines for the Use of Animals in Research and were approved by the University of Oxford Animal Welfare and Ethical Review Board (AWERB). Animal handling procedures were performed by project staff trained and certified by the Zimbabwe Veterinary Association, Wildlife Group (Certificate number: 2014/16) in accordance with Statutory Instrument 409 of1999 (Clause 21A to 21J) amending the Regulations of 1975 to the Dangerous Drugs Act, Zimbabwe. Training was undertaken via attendance at the Chemical and Physical Restraint of Wild Animals Course (run by Zimbabwe Veterinary Association, Wildlife Group and Government

Veterinary Services Wildlife Unit, see http://wildlifecaptureafrica.com/the- course/about-the-course/). Finally, all procedures described above were undertaken with the expressed permission of the Bubye Valley Conservancy.

We positioned a HOBO Weather Station Data Logger (H21-001, Onset Computer Corporation, MA, U.S.A.) in an open area portion of the study site to collect data on wind speed and direction (Fig. 1). The device recorded these measures in addition to ambient temperature and relative humidity at 5-minute intervals across the study period. We also obtained lunar cycle data (e.g., moon illumination and altitude) for the same period using the R package *suncalc* (version 0.5.0; Thieurmel and Elmarhraoui, 2019).

Statistical Analyses

Anemotaxis

To investigate the orientation of lion movement in relation to prevailing wind speed and direction we first calculated the bearing between successive GPS locations to quantify the predominant directional heading of lions during locomotion. We did so using the *earth.bear* function from the package *fossil* (version 0.4.0; Vavrek 2020) in R version 3.6.1 (R Core Team 2019). We then calculated displacement between successive GPS points and used this information to delineate three predominant lion behavioural states including resting, local movement, and relocation (*sensu* Goodall et al. 2019). The hourly displacement for resting and local movement was on average < 300 m. These states were generally absent during periods when a lion moved more than 1 km / hour. Relocation, by comparison, averaged 850 m with an upper limit of > 2 km. We focused our analysis on the relocation state, exemplified by walking and hunting behaviour (Goodall et al. 2019), so that we could consider the influence of wind speed and direction on these behaviours. We restricted our data to points that were at least 1 km from the previous point to reduce the likelihood of including non-locomotory, or highly tortuous, behaviours in our analysis. We also restricted the dataset to hours of darkness (between 20:00 and 04:00 in summer and 19:00 and 05:00 in winter) corresponding to the period when lions are most active and most often engaged in hunting (Stander 1992; Hayward and Slotow 2009).

We summarised wind speed and direction data into hourly means using the function *mean.circular* from the *circular* package (Lund et al. 2017) to calculate average hourly wind direction. We restricted the data to hours in which the wind direction range was less than 60°, when crosswind movement maximises search area (Sabelis and Schippers, 1984), and in which mean wind speed was greater than 0 m/s as anemotaxis is not possible when there is no wind (data summarised in Table S1). We next developed a variable called moonlight based on a binary classification of lunar cycle. We classified the moonlight variable as “light” when illumination was > 10% and the moon was above the horizon, and “dark” when illumination was < 10% or the moon was below the horizon. This approach is similar to that used by Funston et al. (2001), though we were not able to account for prevailing cloud cover. We used the illumination threshold of 10% as the early stages of the new moon are unlikely to provide sufficient light to influence hunting success, as is evident in results reported by Packer et al. (2011).

We then fit generalized linear mixed models (GLMMs) with a binomial distribution and logit link function using the *lme4* package in R (Bates et al. 2015) to predict the probability of crosswind lion movement as a function of wind speed alone (including a quadratic term) as well as wind speed interacting with moonlight, and sex as fixed effects. We fit this model with lion ID, month, and hour nested within month as random effects (to allow inference to the population level and to control for seasonal and time effects). For the response variable, we calculated the acute angular difference between lion bearing and wind direction for each hour and classified angles >45° and <135° as “crosswind” (coded as 1) and angles < 45° and > 135° as “parallel” (coded as 0; see Fig. 2). We then developed nine *a* *priori* models with wind speed alone and in all possible combinations of interactions with lion sex and moonlight. We conducted model selection in R using the MuMin package (Barton 2020) with model ranking via Akaike Information Criterion corrected for small sample sizes (AICc). The model with the lowest AICc was considered the most plausible following the recommendations of Arnold (2010) for small sets (< 10) of *a priori* models. We interpreted predictor effects using odds ratios (OR) and their 95% confidence intervals (CI).

Distance moved

Next, we sought to examine the influence of wind speed on distance moved while controlling for moonlight and sex. We used the *distm* function from the *geosphere* package (Hijmans et al. 2019) to calculate the distance between consecutive hourly locations (rounded to the nearest 100 m) and summarised wind speed into hourly means. As above, we restricted data to hours of darkness. We then developed zero-inflated negative binomial (ZINB) generalised linear mixed models using the R package glmmTMB (Brooks et al. 2017) to predict the distance moved by lions as a function of wind speed alone (including a quadratic term for wind speed) and in interaction with moonlight, and sex as fixed effects. Additionally, we fit these models with lion ID, month, and hour nested within month as random effects to allow inference to the population level and to control for seasonal and time effects. We selected the ZINB GLMM due to non-normality, overdispersion of residuals, and a high proportion of zeros where lions were generally stationary. We considered nine candidate models with the same combinations of predictor variables as used in the anemotaxis analysis. All models were then ranked according to AICc and the model with the lowest AICc selected as the most plausible. We interpreted the results from the conditional model and zero-inflation model separately to distinguish between active and inactive periods of behaviour.

Results

The GPS collars recorded a combined total of 117620 locations for the 29 lions across the study period with an average of 4055 ± 1235 (mean ± sd) locations per individual (Table S1). Mean nocturnal hourly windspeed was 0.74 m/s with a range of 0 – 6.78 m/s. Median nocturnal wind direction was 110°. Further details on wind conditions for each month are shown in Figure S1.

Anemotaxis

The best performing model predicted the probability of a lion moving crosswind as a function of wind speed (Table S2). Interpretation of the parameter estimate illustrates that the odds of lions moving crosswind increased by 11% (OR: 1.11; CI: 1.07-1.15) with every 1 m/s increase in wind speed (Fig. 3). At low wind speeds, lion movement direction was not different from random (~ 50% probability of moving cross wind vs parallel to the wind), whereas at high wind speeds (~ 5 m/s) lions were approximately 75% more likely to move crosswind than parallel to the wind.

Distance moved

The best performing model predicted distance moved as a function of an interaction between wind speed as a quadratic factor, moonlight, and sex (Table S3). The effect of wind speed on distance moved by lions was non-linear and dependent on moonlight and sex. During periods of locomotion, distance moved by females increased linearly with wind speed in dark conditions ($\beta = 0.09 \pm 0.02$ SE, $z = 5.28$, $p < 0.001$; Fig. 4; Table S4a) and non-linearly in moonlit conditions (wind speed: $\beta = 0.01 \pm 0.02$ SE, $z = 0.49$, $p > 0.05$; wind speed^2: $\beta = 0.02 \pm 0.01$ SE, $z = 2.41$, $p < 0.05$; Fig 4; Table S4b). By comparison, distance moved by male lions did not vary significantly with wind speed in dark conditions ($\beta = 0.00 \pm 0.02$ SE, $z = -0.22$, $p > 0.05$; Fig 4; Table S4c) but decreased slightly with increasing wind speed in moonlit conditions ($\beta = -0.05 \pm 0.02$ SE, $z = -2.87$, $p < 0.05$; Fig. 4, Table S4d).

Wind speed had a negative quadratic effect on the probability of remaining stationary (< 50 m movement) for both sexes in light and dark conditions. In light moonlight conditions, lions were more likely to remain stationary as the wind increased from low to moderate speeds. However, at high wind speeds, the probability decreased sharply for both female (wind speed: $\beta = 0.11 \pm 0.03$ SE, $z = 3.67$, $p < 0.001$; wind speed^2: $\beta = -0.07 \pm 0.01$ SE, $z = -5.15$, $p < 0.001$; Fig. 5; Table S5a) and male lions (wind speed: $\beta = 0.21 \pm 0.03$ SE, $z = 6.96$, $p < 0.001$; wind speed^2: $\beta = -0.09 \pm 0.01$ SE, $z = -5.87$, $p < 0.001$; Fig. 5; Table S5b). In dark moonlight conditions, low to moderate winds had little influence on the likelihood of lions remaining stationary. However, both female (wind speed: $\beta = 0.01 \pm 0.03$ SE, $z = 0.36$, $p > 0.05$; wind speed^2: $\beta = -0.04 \pm 0.02$ SE, $z = 2.22$, $p < 0.05$; Fig. 5; Table S5c) and male lions (wind speed: $\beta = 0.1 \pm 0.03$ SE, $z = 3.18$, $p < 0.001$; wind speed^2: $\beta = -0.08 \pm 0.02$ SE, $z = -4.50$, $p < 0.001$; Fig. 5; Table S5d) were much more likely to move as wind speed increased above moderate speeds.

Discussion

Active movement in search of olfactory cues is energetically costly for individual animals (Tucker 1975; Chassin et al. 1976; Halsey 2016). Behavioural strategies that minimise the time spent searching by increasing the probability of detection are expected to afford an advantage to animals that rely on these olfactory cues for communication or foraging (Mcfarland 1977; Norberg 1977; Sabelis and Schippers 1984). Here, we found that lions adjust their movement in response to wind speed and direction in a way that is consistent with the odour detection maximisation strategy described by Sabelis and Schippers (1984). The influence of wind speed on the distance moved by lions, however, varied as a function of sex and moonlight.

As optimal olfactory search theory predicts, when the wind is unidirectional, crosswind movement should increase the geometric size of the search area and thereby maximise the amount of information gained per unit of energy expended (Sabelis and Schippers 1984). Our results showed that both male and female lions were more likely to move crosswind as wind speed increased and that this tendency occurred irrespective of moonlight (Van Orsdol 1984b; Funston et al. 2001b; Packer et al. 2011; Davies et al. 2016). This behavioural strategy suggests that lions are likely to exploit olfactory cues as they navigate their environment and use the wind to their advantage by positioning themselves accordingly to maximise the probability of odour detection. Any anemotactic strategy, however, is predicated on an animal’s ability to sense wind direction. Lions have well-developed mystacial vibrissae which are known to form an important part of the tactile sensory apparatus in many mammals and have also been found to act as flow sensors in some species (Ahl 1986; Yu et al. 2016). In addition to their functional role in prey capture (Kitchener et al. 2010), lion vibrissae might therefore serve as wind sensors to facilitate anemotaxis, though, further studies would be required to confirm this. While crosswind movement is optimal when the wind is unidirectional, this is not the case when direction varies more than 30° from the mean (Sabelis and Schippers 1984). Above this level, odour detection is maximized via upwind or downwind movement. Hourly wind direction in the BVC rarely fluctuated more than 30° during moderate to high wind speeds. Thereby, we were unable to examine whether lions adjust their anemotactic strategy in response to highly variable wind directions.

In addition to anemotactic behaviour, we also found that female lions tended to move farther with increasing wind speeds. In light moonlight conditions, this behaviour appears to be restricted to stronger winds as no increase in movement distance was evident at lower wind speeds (< 2 m/s). In addition to travelling farther, females were also more likely to move in strong winds than in low to moderate wind speeds. The distance moved by male lions, by comparison, was not influenced by wind speed in dark conditions and decreased slightly with increasing wind speed in light moonlight conditions. However, like female lions, males were more likely to move when wind speeds were high. Movement distance provides a reasonable representation of the relative amount of energy invested in searching at a particular time as more energy must be spent on locomotion in order to cover greater distances (Norberg 1977). The net benefit of actively searching for prey and olfactory information on conspecifics during stronger winds might therefore outweigh the net benefit of doing so during calm conditions due to the greater search efficiency afforded by crosswind movement (Norberg 1977; Sabelis and Schippers 1984). Lions may adopt an active search hunting strategy more often than the sit-and-wait hunting technique in such conditions (Higginson and Ruxton 2015), though assessment of this hypothesis requires further investigation. To date, the increased lion hunting success that has been reported for darker and more windy conditions has only been attributed to reduced detection by prey as darkness, moving vegetation, and the noise created by wind can conceal predator approach (Leuthold 1977; Van Orsdol 1984). Our work reveals an additional plausible explanation for greater success under these conditions in that lions might benefit from increased prey detection due to their crosswind search strategy. A possible reason for the difference in the distance moved ~ wind speed relationship between males and females is that the driving factors underpinning behaviour differ between the sexes. Females are primarily motivated by resource acquisition whereas male behaviour is shaped more by access to and protection of females (Emlen and Oring 1977; Funston et al. 1998). Male lions might therefore need to travel farther regardless of windspeed in order to locate mates and patrol their territories while females may choose to reduce search behaviour in calm conditions in favour of other modes of resource acquisition (Elliott et al. 1977; Higginson and Ruxton 2015). However, our results show some evidence that males do take advantage of strong winds as they are more likely to engage in locomotion when wind speeds are high. Sex differences in travel distance among lions have been documented in a previous study where males were found to travel more than twice as far per day compared to females (Hayward et al. 2009). Our results suggest that in stronger winds, females tend to travel similar distances than males and that wind speed could be an important factor driving their movement behaviour.

We acknowledge that our study presents correlative evidence of crosswind movement by lions and therefore encourage more detailed mechanistic studies that quantify the impact of wind dynamics on all aspects of lion behaviour. A logical extension of our research would be to focus examinations on dynamic micro-habitat selections. The scale of our GPS locations (i.e., hourly fixes) did not facilitate such analytical frameworks. Future studies investigating animal movement and orientation relative to wind would benefit from using accelerometer and magnetometer data loggers, where possible, to provide high resolution information on animal posture and orientation relative to magnetic north (Fourati et al. 2011; Bidder et al. 2015). We also acknowledge that lion locomotion revealed by GPS telemetry alone may not always represent search behaviour. Lions might move farther to reduce the risks of inter or intra-specific conflict, for example. Distinguishing between active search and non-search locomotory behaviours is challenging to do remotely. Though we focused this study only on lion behavioural responses to wind, it is important to note that prey also alter their behaviour to mitigate the risks of predation (Clark 1994). Knowledge of how prey species might adapt to wind-induced variation in predation risk is therefore a vital component required in gaining a more complete understanding of the effects of wind on predator – prey dynamics. We therefore recommend this as a focus of future research on the topic.

Investigating the influence of environmental factors on animal behaviour is essential to improving our understanding of species ecology. While research on the effects of abiotic variables, such as temperature, is common, relatively few studies have considered the effects of wind speed and direction on terrestrial megafauna (Cherry and Barton 2017). Analysis of long-term datasets from across the globe has revealed that near-surface wind speeds are currently decreasing and could result in a -0.7 m/s change over the next 50 years, should the current trend continue (McVicar et al. 2012). This raises important questions about the impact of such changes on animal olfactory search behaviour and the consequences for foraging and communication. Our study has revealed that lions likely employ specific behavioural strategies that allow them to benefit from wind through increased search efficiency. This finding makes an important contribution towards current knowledge on the role of olfaction in the species and suggests that wind could be an important factor influencing lion activity patterns. It is reasonable to expect that similar patterns of behaviour might also be observed among other large carnivore species that rely on olfaction. Ultimately, our study highlights that wind might be more important for terrestrial predators than previously documented by science, although widely appreciated by field naturalists.

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Figure legends

Figure 1. Study area in the Bubye Valley Conservancy, southern Zimbabwe. Inset map shows location of the study site in southern Africa.

Figure 2. Classification of African lion (*Panthera leo*) movement direction relative to wind direction for the logistic regression analysis of the relationship between lion movement direction (relative to wind direction) and windspeed in the Bubye Valley Conservancy.

Figure 3. Probability of African lion (*Panthera leo*) crosswind movement with increasing wind speed as inferred from GPS tracking in Bubye Valley Conservancy, Zimbabwe from February to December 2014.

Figure 4. Distance moved by female and male lions (*Panthera leo*) in relation to increasing wind speed in moonlight (i.e., dark and light conditions) as inferred from GPS tracking in Bubye Valley Conservancy, Zimbabwe from February to December 2014.

Figure 5. Probability of female and male lions (*Panthera leo*) remaining stationary (< 50 m movement) in relation to increasing wind speed in dark and light moonlight conditions as inferred from GPS tracking in Bubye Valley Conservancy, Zimbabwe from February to December 2014.

Figures

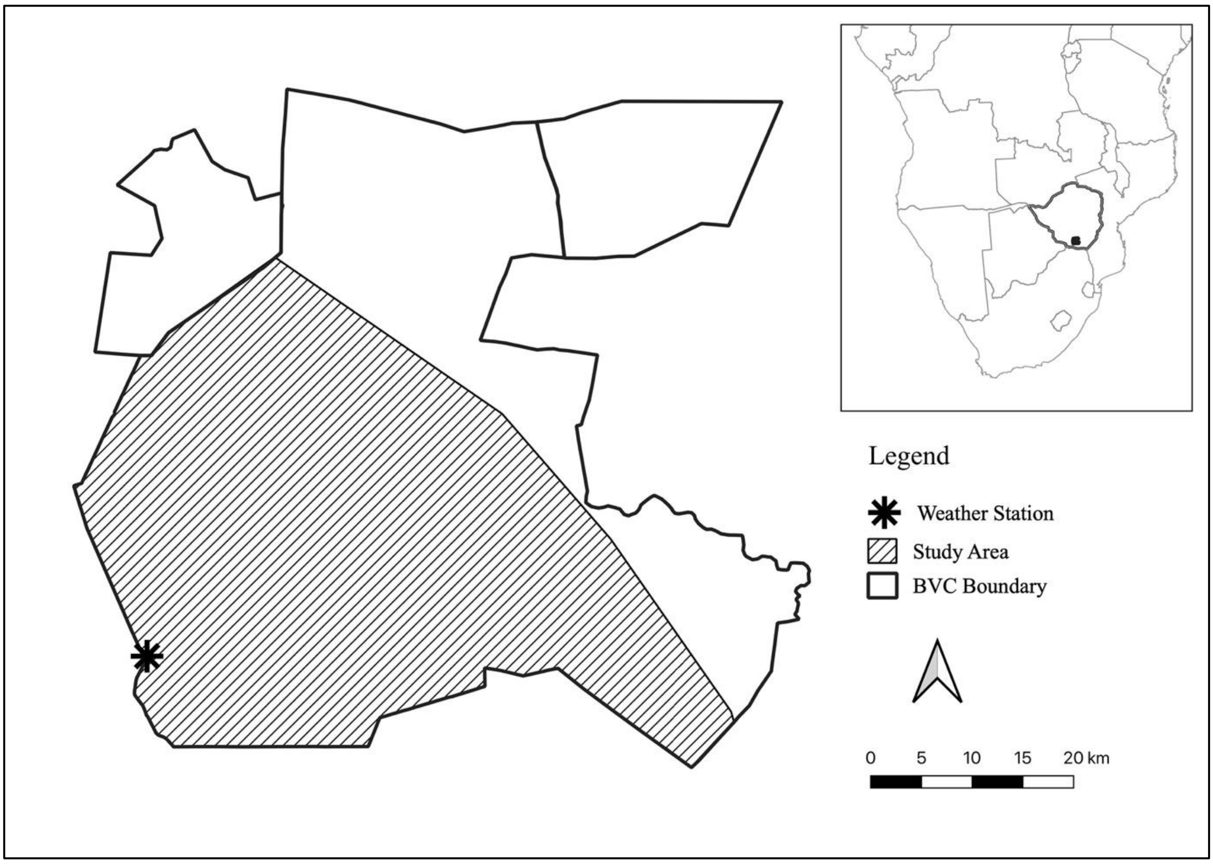
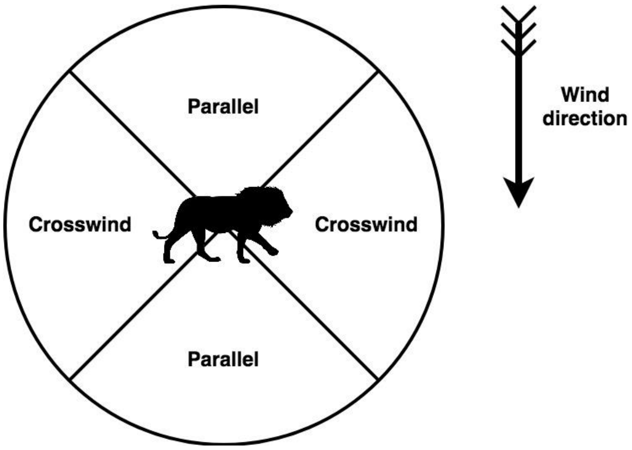


Figure 1



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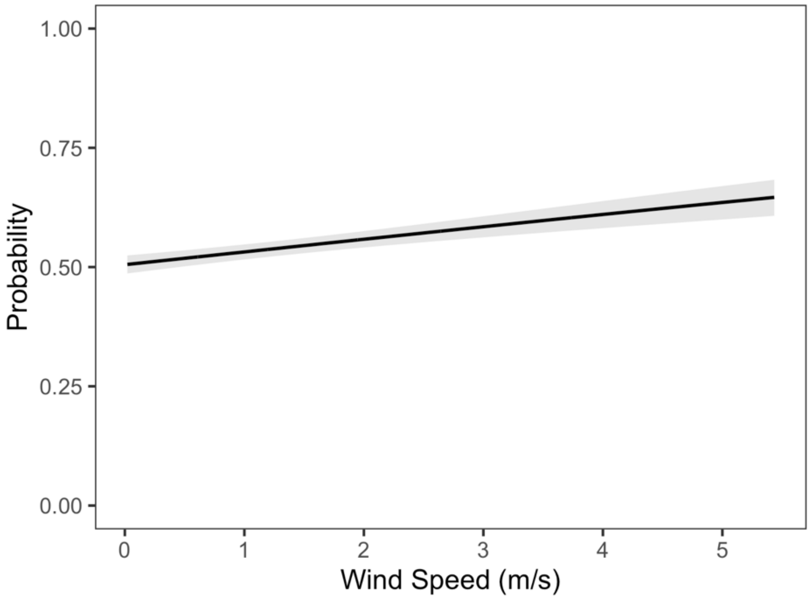

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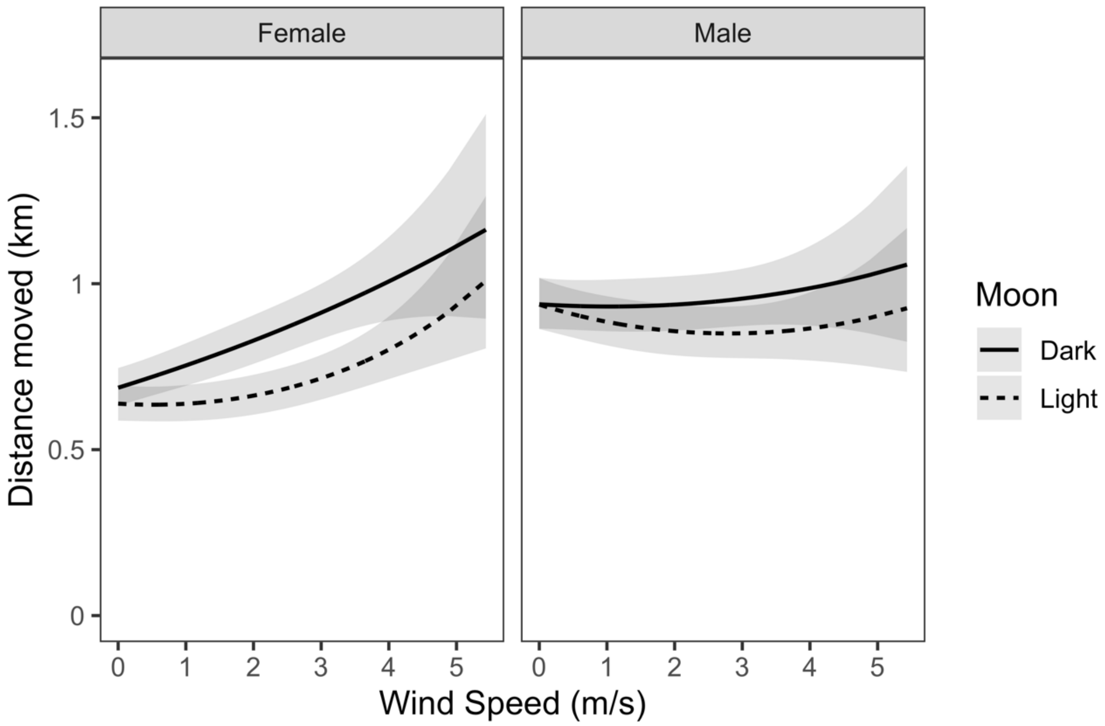

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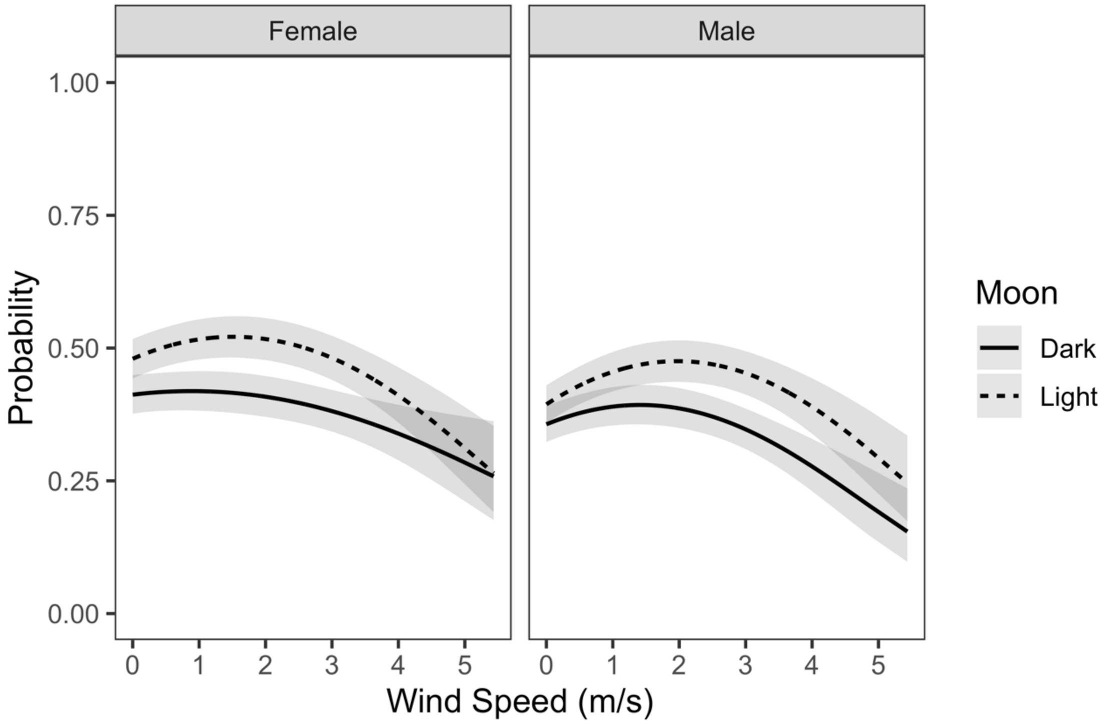
596 Figure 4.



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598 Figure 5.