How air temperature affects flight initiation distance in arid-zone birds

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Abstract

Arid zones, such as the Kalahari in southern Africa, are experiencing an increase in the number of hot days, as well as in the intensity of heat waves. Research is being conducted to try and understand how increasing temperatures will impact bird communities and population persistence in these areas. Understanding the mechanisms through which birds are vulnerable to climate change is key to answering these questions. This study investigated how changes in air temperature affect arid-zone birds' response to predators. The flight initiation distances (FID), i.e. the distance from a predator when the prey initiates escape, of eight bird species in the Kalahari were measured over a range of air temperatures during October and November 2015. The results from this study show a negative relationship between air temperature and FID. This relationship was weak across the full range of temperatures observed during the study period (11.9 ^{o}C – 40.4 ^{o}C), with a large amount of variability in FID not explained by air temperature. However, high air temperatures (> 35 ^{o}C) were important in explaining some of the variation in FID. Starting distance, time of day, bird species, plant species, bird location (on the ground / in the canopy / at the top of the tree / in a dead tree), bird exposure (whether the bird was in the sun or in the shade) and bird activity (whether mobile / stationary) were consistently found to explain some of the variation in FID in this dataset. The relationships between the behavioural variables (plant species, bird location, bird exposure and bird activity) and air temperature were investigated and revealed a potential mechanism through which air temperature may also indirectly be affecting FID. The reduction in FID at high air temperatures, and thus the potentially increased risk of predation, may have negative consequences for these species in the Kalahari in light of rising air temperatures associated with climate change.

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Plagiarism declaration

I know the meaning of plagiarism and declare that all of the work in the dissertation, save for that which is properly acknowledged, is my own.

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Introduction

Most climate change models predict severely negative consequences for biodiversity (Bellard *et al*. 2012). One of the components of climate change is increasing air temperatures. Evidence of rising temperatures has emerged for areas around the globe. Mean global temperature trends show increased warming since the end of the 20th century and in particular from the mid-1960s (Brohan *et al*. 2006; Lugina *et al*. 2006; Smith *et al*. 2008; Karl *et al*. 2015). South Africa too has experienced a general warming since this time. All weather stations investigated in South Africa over the period 1962-2009 showed an increase in hot extremes and decrease in cold extremes (Kruger and Sekele 2013). The areas within South Africa that have relatively warmer thermal regimes – the Lowveld, east coast and dry western interior – experienced the largest increases in warm extremes (Kruger and Sekele 2013). Temperature increases have also been measured in terms of their implications for species. Cunningham *et al*. (2013a) found an increase in the annual number of hot days (maximum air temperature > T_{thresh}) and in the maximum intensity of biologically meaningful heat waves for Southern Pied Babbler *Turdiodes bicolor* and Common Fiscal *Lanius collaris* in north-western South Africa between 1961 and 2010. Although evidence of climate change is now unequivocal, the full extent of the impacts of these and future changes on species has yet to be determined.

Thermoregulation

The habitats that animals live in carry physiological consequences (Huey 1991). Changes in environmental temperatures may benefit some species in some areas, while increasing the thermoregulatory challenges experienced by others. While climate warming may increase activity time for ectotherms in temperate areas, potential activity may be reduced for taxa in tropical and desert areas and their potential for behavioural thermoregulation will largely depend on the availability of shade (Kearney *et al*. 2009). Environmental temperatures have important implications for endotherms, too. For example, when environmental temperatures are higher than an endotherms' body temperature, they are unable to lose heat passively to the environment, with the result that evaporative water loss becomes important for the loss of both metabolically generated heat, as well as heat absorbed from the environment (Calder and King 1974; Wolf 2000). In trying to manage their body temperatures, small, endothermic animals can be left with water or energy deficits (Wolf and Walsberg 1996). Energy used for thermoregulation is also no longer available for other activities like reproduction (Wolf and Walsberg 1996). Even moderate increases in air temperature as a result of climate change will greatly increase water loss rates of small birds, which could lead to lower survival times during inactive periods (Wolf 2000). McKechnie and Wolf (2010) predict that increasing air temperature maxima, as a result of climate change, will decrease the ability of birds to use facultative hyperthermia to save water, and that a large number of birds will die because they are not able to dissipate heat fast enough. Living in environments with extreme high temperatures can therefore come with significant thermoregulatory costs.

When air temperatures pose thermoregulatory challenges, animals can adapt their behaviour to assist in keeping their body temperatures within acceptable limits. This can occur at both low and high temperatures. For example, Short-toed Treecreepers *Certhia brachydactyla* select sunlit foraging patches at low temperatures to save energy; however the limited temperature range within which this behaviour occurs points to there being a trade-off with increased predation risk as a result of the birds being more visible in the sun (Carrascal *et al*. 2001). In hot temperatures, birds need to reduce their metabolic and environmental heat gain. The use of thermally buffered microhabitats can limit the heat a bird absorbs from its environment and reduce evaporative water loss. Verdins *Auriparus flaviceps* can reduce their rate of evaporative water loss substantially by choosing microsites out of the wind and sun in summer (Wolf and Walsberg 1996). Wolf (2000) illustrated how spending time in shaded microsites could greatly increase the survival times of Verdins that are not foraging. Shady microsites are also chosen by birds in the hot and arid southern Kalahari, where they show increased preference for trees with the highest density of shade on hot days and at the hottest times of day (Martin *et al*. 2015). Such microsites can be significantly cooler than shade air temperatures (Wolf *et al*. 1996), and can help to reduce water loss rates (Wolf 2000). In addition to shifting activities to cooler microhabitats as air temperatures increase, behavioural changes can also include a reduction in the amount and rate of activity, including foraging and parental care activities (Ricklefs and Hainsworth 1968; Austin and Miller 1982). For example, Cactus Wrens *Campylorhynchus brunneicapillus* in the Lower Sonoran desert, Arizona reduced nest visits when absorbing temperatures exceeded 35°C (Ricklefs and Hainsworth 1968). Although behavioural changes can help to mitigate the impacts of environmental temperatures the changes are not without consequences themselves.

Maintaining body temperature within critical limits in extreme environments has consequences for the fitness of individuals and populations. In examining the links between climate warming and lizard extinctions, Kearney (2013) found that climate warming could cause populations to decline due to impacts on fecundity and mortality rates, although life history, behaviour and habitat played a role too. Changes in behaviour driven by the avoidance of heat stress can have fitness consequences for birds too. In the southern Kalahari, high air temperatures were found to have negative implications for the maintenance of body mass in Southern Pied Babblers *Turdoides bicolor* as a consequence of reduced foraging efficiency (du Plessis *et al*. 2012). The foraging success of Southern Fiscals was reduced by ~50% when switching their foraging location to shaded perches during the afternoon on hotter days (Cunningham *et al*. 2015). Increased warming with climate change may result in greater fitness costs to species as temperatures rise.

Escape behaviour

One of the behaviours that might be traded-off with thermoregulation is predator avoidance. Successfully fleeing from predators is a matter of survival for prey species. Ydenberg and Dill (1986) developed an economic model which looks at the decisions prey animals make about when to flee from an approaching predator. Fleeing from a predator has the benefit of increasing chances of survival, but it also has costs. The distance at which prey choose to flee will depend on the relative benefits and costs of doing so. Ydenberg and Dill's (1986) model shows that as the costs of remaining increase, flight initiation distance (FID) increases and as the costs of fleeing increase FID decreases. The optimal flight distance is predicted to be where the costs of remaining and fleeing are equal. Blumstein (2003) modified the model to include a minimum distance, below which animals will always respond to threats, and a maximum distance, above which animals will not flee.

The costs of keeping cool are likely to affect escape behaviour. As air temperatures rise to levels that pose thermoregulatory challenges to endotherms, the costs of fleeing can be hypothesised to increase. If for example an animal is in a cool microsite when a predator approaches, the cost of fleeing will increase with air temperature because the animal will not only be exposed to greater environmental temperatures if it has to move to a hotter microsite, but will also generate additional metabolic heat through fleeing. The rise in body temperature above critical limits is a threat to the animal. Cooling down again after flight may also present a significant challenge, particularly in hot, arid environments where evaporative water loss through cooling may lead to dehydration. Thus, rising temperatures are predicted to result in increasing costs of fleeing and a decrease in flight initiation distance (Figure 1).

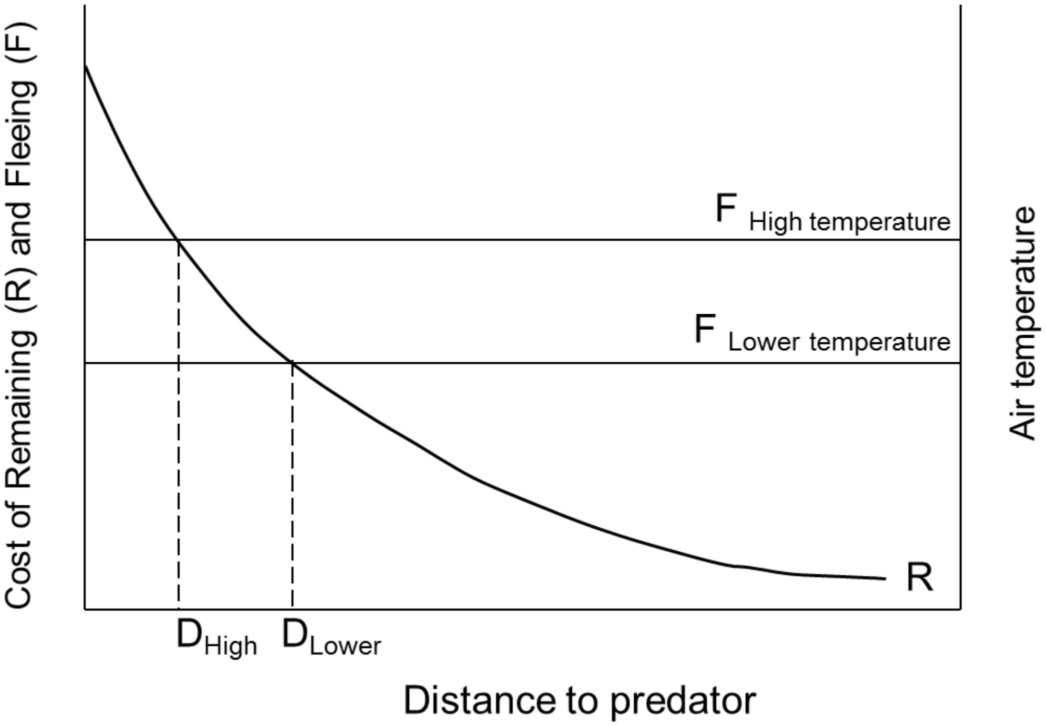

Figure 1: The costs and benefits of fleeing from a predator at different air temperatures. As air temperatures rise to levels that pose thermoregulatory challenges to animals the cost of fleeing is likely to increase. Prey are predicted to flee when R (Cost of Remaining) > F (Cost of Fleeing), with optimal flight initiation distance at D. At higher air temperatures the distance at which prey will flee from a predator is predicted to decrease (D_{Lower} – D_{High}) due to the increasing thermoregulatory costs of fleeing. (Adapted from Ydenberg and Dill (1986)).

Flight initiation distance

Flight initiation distance (FID), the distance from a predator when the prey initiates escape, has been linked to a number of characteristics in birds. Species with a higher basal metabolic rate for their body mass were found to have longer FIDs (Møller 2009). Blumstein (2006) also found a relationship between FID and body size, with larger bird species initiating flight at longer distances than smaller species. No relationship, however, was found between FID and characteristics such as longevity, habitat density or clutch size (Blumstein 2006). Blumstein *et al*. (2003) found FID to be a species-specific trait for eight species of shorebirds in Australia, while Carrete and Tella (2010) found strong individual consistency in FID in Burrowing Owls *Athene cunicularia* in Argentina. An individual bird's susceptibility to disturbance may then influence how they distribute themselves among breeding sites, with potential ecological and evolutionary implications as human disturbance of habitats increases (Carrete and Tella 2010). Møller (2008) predicted that bird species with longer FIDs would have a higher frequency of declining populations than species with short FIDs where there is increased human impact on habitats, as they would suffer more often from disruption of their activities. This predicted negative relationship between population trend and FID was found to occur in Europe and Australia, but not in North America (Møller 2008; Møller *et al*. 2014). While FID is related to susceptibility to predation, Møller *et al*. (2015) found that it was also related to the risk of brood parasitism by the common cuckoo *Cuculus canorus*. FID is thus a complex measure of risk-taking (Møller *et al*. 2015).

FID has been measured in a number of studies, using similar methods (e.g. Blumstein 2003, Blumstein *et al*. 2003, Blumstein 2006, Møller 2008, Møller 2009, Carrete and Tella 2010, Weston *et al*. 2012, Møller *et al*. 2015; Appendix A). In these studies birds were observed from a distance (which was either pre-determined and standardised per study, or recorded separately for each FID measurement) and then approached by a human at a steady walking pace. The horizontal distance (from the observer) at which the bird flees was recorded. If the bird was located in vegetation, the height of the bird above ground when it took flight was also recorded in some studies. FID was then recorded as the horizontal or Euclidian distance, which was calculated as the square root of the sum of the squared horizontal distance and the squared height.

Main research aim and hypothesis

In order to predict what the consequences of climate change on bird communities in arid-zones will be, we need to gain a better understanding of the physiological implications, as well as how the behaviour of these birds will change with rising air temperatures. This study focussed on a behavioural aspect of this complex question, namely anti-predator behaviour. My main research aim was to determine whether air temperature has an effect on anti-predator behaviour, measured in terms of flight initiation distance (FID), in arid-zone birds. I predicted that an increase in air temperature would result in a decrease in FID as the cost of fleeing increases with air temperature due to thermoregulatory constraints. Due to the variety of factors that have been found to affect FID in other studies I also wanted to understand the relationship between air temperature and other explanatory variables influencing FID.

Methods

Ethics statement

The methods used in this study were approved by the University of Cape Town Science Faculty Animal Ethics Committee (Approval number 2015/V11/SC) and Northern Cape Department of Environment and Nature Conservation (Permit number: FAUNA 1489/2015). The study was carried out on private land, with permission from the landowners.

Study site

The study took place on Murray Guest Farm (11 000 ha; 26°59'S, 20°52'E), 12 km east of the town of Askham in the Northern Cape province of South Africa, south of the dry Kuruman riverbed (Figure 2). Murray Guest Farm lies in the Kalahari Desert, a semi-arid savanna. Dorper sheep and cattle are farmed on the property. Sand dunes run across the farm at regular intervals, creating a series of dune streets in the troughs between the dunes. Transects for the study were established in the dune streets within an area 5.5 km south of the Kuruman riverbed (Figure 2). Data collection took place in this area of the farm to try and standardize conditions as far as possible and to encompass vegetation with trees in it, as well as a diversity of bird species; the further south from the Kuruman riverbed the farm extends, the fewer trees occur. The vegetation in the study area was dominated by small, shrubby *Rhigozum trichotomum*, with larger, bushy *Senegalia mellifera* and taller *Boscia albitrunca* and *Vachellia erioloba* trees.

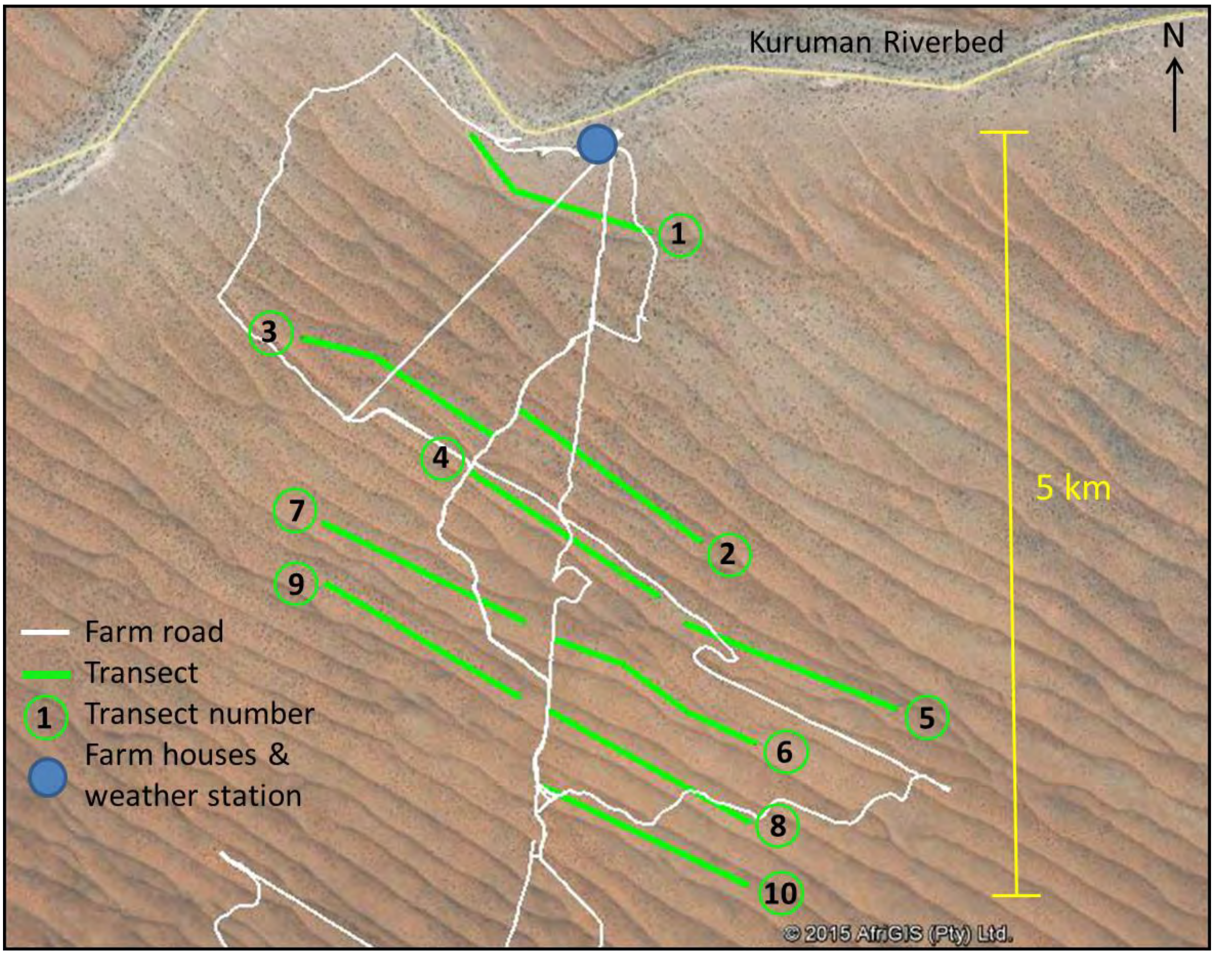

Figure 2: Location of Murray Guest Farm in the Northern Cape Province of South Africa (top). Layout of transects for the study on Murray Guest Farm (bottom; background images from Google earth).

Study procedure

The study took place from 1 October to 24 November 2015. Ten transects, each 1 500 m long, were established on the farm after arrival (Figure 2). Each transect, with the exception of one (number 3 in Figure 2), was visited either seven or eight times over the course of the fieldwork period at a range of different air temperatures. Transect three was only used twice as it was found that this transect did not have enough trees of a suitable size (trees were sparse and mostly taller than 4 m). A repeated measures design was chosen to control, to a limited extent, for variation in FID that was attributable to variation in habitat structure. In addition, this design maximised data collection in an area with limited suitable habitat. The dune streets on the property lent themselves to the transect design. Transects were placed in dune streets that were chosen for the presence of trees less than 4 m tall as it was difficult to flush birds from taller trees. Data collection was carried out in three two-hour sessions in a day: an early morning session from 07:00 to 09:00, late morning session from 10:00 to 12:00 and an afternoon session from 14:00 to 16:00. The session from 14:00 to 16:00 was chosen to coincide with the hottest time of the day as measured by weather station air temperature data. Only one transect was walked per session. Each transect was used only once in a week (except for transect 6 that was, on one occasion, used twice in a week) to reduce the likelihood that birds in a particular area would become habituated to the procedure. Transects were walked in alternating time sessions over the course of the study period so that FID measurements along a particular transect were spread throughout the day to avoid confounding the effects of time of day with transect, e.g. Transect 1 was used twice in an early morning session (07:00 – 09:00), twice in the late morning session (10:00 – 12:00) and three times in an afternoon session (14:00 – 16:00) across the course of the study period.

To measure FIDs along a transect, two people (myself and an assistant, Michelle Thompson), wearing neutral-coloured clothing, would walk slowly down the dune street scanning the ground, bushes and trees for birds using binoculars. When a bird was observed we would stop. If there was no straight line access from which to approach the bird (e.g. a large bush between ourselves and the bird in a tree behind it), we would carefully manoeuvre ourselves until there was a straight path we could use to reach the bird. Michelle would then look at the bird through binoculars to confirm the species and its behaviour while I measured the starting distance between us and the bird using a Nikon Laser rangefinder. Starting distances of less than 100 m were used in this study as it was unclear whether birds approached from distances > 100 m were flying away due to our approach or other factors. The date, time, session (early morning, late morning or afternoon), transect number and starting distance were recorded using a customised data collection programme in CyberTracker, a GPS Field Data Collection System (CyberTracker 3.389), which had been loaded onto an Android smart phone (Samsung Galaxy Fame GT-S6810).

We would then walk at a brisk pace (approximately 1.5 $m.s^{-1}$) directly towards the bird until it flew or ran away. We would stop walking as soon as the bird left the tree, bush or patch of ground it was on. In cases where there were actually or potentially more than one species in a tree, instead of stopping when the bird took flight we would drop a marker (clear plastic freezer bags filled with white cake flour that were visible against the orange coloured sand of the Kalahari Desert) on the ground each time a species flew and continue walking towards the tree. This was done so that the approach would be continuous for all species in the tree. The markers were used to identify the position I needed to return to in order to measure the FID for each species.

After the bird had been approached, the remaining details about the bird were entered onto CyberTracker. This included the bird's activity before we started walking towards it (whether it was mobile or stationary), the bird's location (e.g. on the ground / in the canopy / at the top of the tree / in a dead tree), the species of tree/shrub the bird was in / under and the bird's exposure (whether it was in the sun, full shade or dappled shade). Exposure data were later consolidated into two categories: sun or shade (which included full shade and dappled shade) for analysis. In cases where the bird was not observed clearly before the approach, no bird activity or exposure data were recorded.

The oblique FID (the distance from myself, at eye height, to the point from which the bird took flight or ran away) was then measured directly using a Nikon Laser rangefinder and recorded for each species. Where oblique FIDs were not able to be measured directly with the rangefinder (due to e.g. branches obstructing the rangefinder's ability to measure the correct distance, or the distance being < 10 m, outside the capability of the rangefinder), horizontal and vertical distances to the bird were determined with a rangefinder where possible, or by pacing out the horizontal distance or estimating the height where the rangefinder could not be used. These distances were then used to calculate the oblique FID. If the bird was located above me: $FID_{oblique} = \sqrt{{FID_{horizontal}}^{2} + (bird\ height - my\ eye\ height)^{2}}$, or if the bird was located below my eye height: $FID_{oblique} = \sqrt{{FID_{horizontal}}^{2} + (my\ eye\ height\ - bird\ height)^{2}}$. When there was more than one individual of a species in the same location, the FID of the bird that flew first was recorded.

To minimise the likelihood that individual birds were included in the study more than once along a transect in a session, birds of the same species in the vicinity (i.e. approximately 10 minutes or 200 m) of an FID recording were not approached for further data collection, unless we had clear reason to believe it was a different individual.

Some FID values were also measured opportunistically during the study period while collecting data for another study. The opportunistic FID data were collected in the same area of the farm and in same way as the procedure described above, but not on the transects highlighted in Figure 2. I included these data as their own level within the variable "Transect".

Temperature data

Air temperature was measured at five minute intervals using a portable weather station (VantagePro 2, Davis Instruments, Hayward, CA, USA) that was set up in an open area of veld adjacent to the farmhouses for the duration of the study (Figure 2). The weather station was approximately 500 m from the closest transect (No.1 on Figure 2) and 5 km from the furthest (No. 10 on Figure 2). The time that each FID value was recorded was rounded to the nearest five minutes and linked to the corresponding air temperature for that time.

Operative environmental temperatures in representative shaded and sunny microsites were measured using black-bulb thermometers. Each black-bulb thermometer consisted of an iButton^{TM} temperature data logger (Fairbridge Technologies, Sandton, South Africa) enclosed by two hollow 30-millimetre-diameter copper hemispheres that were painted black on the outside and glued together to make a sphere. The iButton^{TM} was secured inside the black-bulb using a clip or wire fastened to the side of the copper sphere with glue. Wire was drawn through a small hole in the base of the black-bulb to wind around the branch of a tree or to stick into the ground to keep the black-bulb thermometer in place. The thermometers were placed within the canopies of four *Boscia albitrunca*, four *Vachellia erioloba* and four *Senegalia mellifera* trees, as well as on the ground below each of these trees to measure the difference in shaded temperature in these microsites. Thermometers were also placed on the edges of the canopies of two trees of each species in the sun, in three dead trees in the sun and in three open locations on the ground in the sun. The black-bulb thermometers were left in place to record temperatures at ten minute intervals from 9 October to 22 November 2015. Temperatures were recorded at ten minute intervals (not five minute intervals as recorded by the weather station) due to space limitations on the iButtons^{TM}. The iButtons^{TM} were removed once from each location during the recording period to download the data and returned the same day. Temperature readings from the times when the iButtons^{TM} were removed from their locations to download data were excluded from analysis.

Statistical analysis

All analyses were conducted in the statistical programme R (R Core Team 2015), using the packages lme4 (Bates *et al*. 2015), LMERConvenienceFunctions (Tremblay *et al*. 2015), MuMIn (Barton 2015) and multcomp (Hothorn *et al*. 2008). T-values < -2 and > 2 in the general linear mixed models and p-values < 0.05 were taken as statistically significant.

FID data analysis

Data from eight bird species accounted for the majority (n = 633) of the total (n = 771) FID measurements taken during the study. The eight species were: Scaly-feathered Finch (*Sporopipes squamifrons*; n = 137), Black-chested Prinia (*Prinia flavicans*; n = 91), Chestnut-vented Tit-Babbler (*Parisoma subcaeruleum*; n = 83), Cape Turtle Dove (*Streptopelia capicola*; n = 78), Fawn-coloured Lark (*Calendulauda africanoides*; n = 71), Kalahari Scrub-Robin (*Cercotrichas paena*; n = 65), Yellow-bellied Eremomela (*Eremomela icteropygialis*; n = 56) and Sociable Weaver (*Philetairus socius*; n = 52). No more than 18 FID measurements were recorded for any other individual species and other species were therefore excluded from all analyses due to insufficient data for comparative purposes.

A general linear model of FID as a function of starting distance and bird species (explanatory variables found in other studies to affect FID, e.g. Blumstein 2003 and Blumstein *et al*. 2003) was used to compare log-transformed and untransformed FID data. Residuals conformed better to model assumptions where FID was not transformed. Data were therefore left untransformed for all analyses.

General linear mixed models were used in all analyses of the FID data. A random term for transect identity was incorporated into all models to account for variation that may exist between transects due to differences in habituation to human movement, as well as any other systematic differences that might have been present in the FID data that were collected opportunistically (off-transect). Transects varied in their background exposure to human activity due to being varying distances from farm buildings or animal troughs.

Blumstein (2003) recommends including starting distance as a co-variate in models of FID due to its documented effect on FID. I tested for this effect in my data in order to verify that starting distance should be included in all models in this study. In a general linear mixed model (random term for transect) starting distance had a significant positive effect on FID (t = 17.66) overall for the eight focal bird species (n = 633; Figure 3). There was an estimated 0.49 m increase in FID for each 1 m increase in starting distance (95% CI: 0.43 – 0.54 m). I therefore included starting distance in all models of FID.

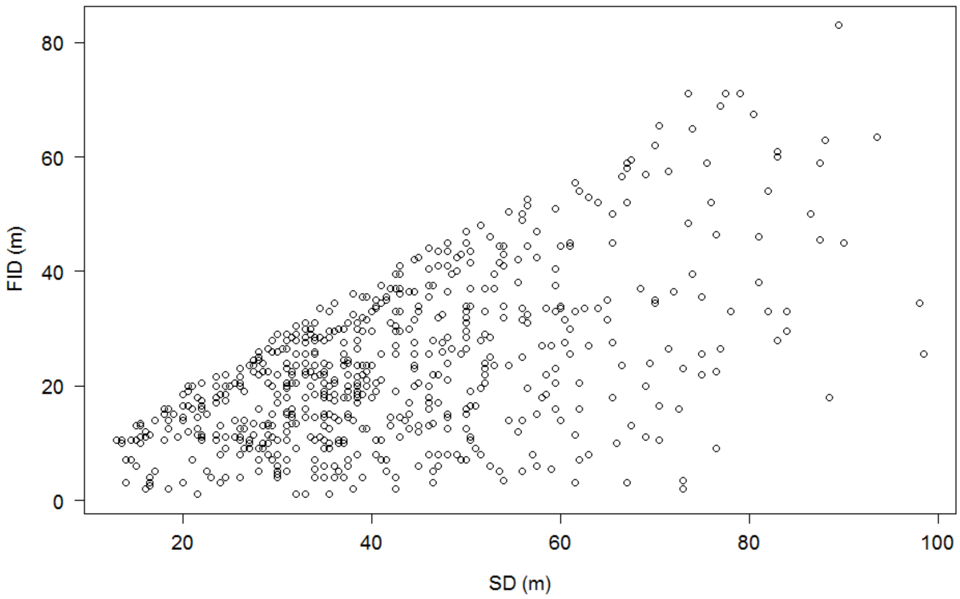

Figure 3: The significant positive effect of starting distance on the overall flight initiation distance (FID) of eight focal bird species (n = 633) in the Kalahari Desert during October and November 2015.

The relationship between air temperature and FID

The effect of air temperature on FID was investigated using all data collected across the full range of air temperatures, as well as separately looking at data collected at air temperatures of 35 ^{o}C and above, and at data collected at air temperatures below 35 $^{\circ}$C. I used 35 $^{\circ}$C as a threshold because several studies suggest behaviour and/or fitness of arid-zone birds changes above temperatures in the mid-30s (e.g. Austin and Miller 1982, du Plessis *et al*. 2012, Cunningham *et al*. 2013b). Air temperature might be expected to have a quadratic relationship with bird behaviour as temperatures move from cold to comfortable to hot, but a general linear mixed model of FID as a function of air temperature had a lower AIC value (4899.41) than a model fitted with a quadratic term for air temperature (AIC value of 4906.96) by > 2 units. Air temperature was therefore fitted as a linear term in all analyses.

Exploring indirect effects of air temperature on FID via effects on behaviour

I explored mechanisms through which air temperature may affect FID by examining the relationships between FID and the behavioural variables (three variables related to microsite choice: plant species selected, bird location and bird exposure; plus the activity of the bird prior to approach, i.e. mobile versus stationary) and then the potential link between these behavioural variables and air temperature. The relationships were investigated individually by fitting general linear mixed models of FID, and separately of air temperature, with each of the behavioural variables. I used all data from the eight focal bird species for these analyses (except the levels within the variable being analysed for which there were insufficient data, e.g. I excluded an observation taken from a particular tree species, when analysing the plant species variable, if there was only one FID measurement from that tree species). This process was carried out using data from the full range of air temperatures and then repeated for each of the subsets of data above and below 35 $^{\circ}$C. Starting distance was included as a co-variate in all FID models, and transect identity was included as the random factor.

Full model analyses: the role of air temperature together with other factors affecting FID

To evaluate how different variables combined to best explain variation in FID, a model selection approach was used. I used the dredge function in the R package ‘MuMIn’ to compare all nested models within a global model containing the following factors: air temperature, starting distance, time of day, bird species, plant species, bird location (ground / canopy / tree top / dead tree), bird exposure (whether the birds were in the sun or shade) and bird activity (whether birds were mobile or stationary prior to approach). Models were compared using AICc (Akaike’s Information Criteria, adjusted for small samples) and top models were selected on the basis of having an increase in AICc of less than 2 units above the best-fit model.

FID measurements where bird exposure and activity had not been recorded were excluded from the models. Observations were also excluded from analysis if they represented rare data within a particular variable (e.g. the only FID measurement for a particular plant species).

I first evaluated the fit of these models in a data set including the full range of air temperatures observed. In addition I explored which models best fitted subsets of the data for observations at or above 35 ^{o}C and observations below 35 ^{o}C. Bird exposure was not included as a variable in the analysis of observations at or above 35 ^{o}C as there were only two observations of birds in the sun in this subset.

To explore differences between bird species in terms of which variables explained variation in FID, I conducted an additional set of analyses, analysing subsets of data for each of the 8 focal bird species separately using the same model selection approach described above. Bird location, bird exposure and bird activity were included in the global models for each species where sufficient data for these variables existed for a particular species. Where variables had to be excluded from the global model for a species due to insufficient data, these are indicated in the results.

Black-bulb data analysis

Only iButton^{TM} temperature readings from the three time sessions during which FID data were collected were used in analysis, i.e. early morning (07:00 – 09:00), late morning (10:00 – 12:00) and afternoon (14:00 – 16:00). Temperature readings from each location category, e.g. the four sets of measurements from within the canopies of four *Boscia albitrunca* trees, or the three sets of measurements from black-bulbs placed in dead trees, were inspected graphically so that any abnormal sequences of readings due to e.g. iButton^{TM} malfunctions, could be removed. Temperatures for each date and 10-minute time interval were then averaged within each location category.

Data were divided into two groups based on the exposure categories used in the FID analysis (i.e. shade and sun). Black-bulb temperature data were analysed using general linear models. Two models were fitted to investigate the effect of (1) location (ground vs canopy) and (2) plant species (*Boscia albitrunca*, *Senegalia mellifera* or *Vachellia erioloba*) on black-bulb temperature in the shade. A third model was fitted to data from black-bulbs that had been placed in sunny locations to investigate the effect of placement (i.e. whether on *Boscia albitrunca*, *Senegalia mellifera*, *Vachellia erioloba*, dead tree or open ground) on black-bulb temperature.

A model selection approach was then used to assess the effects of location, plant species and placement on the relationship between black-bulb temperature and air temperature. The global model for black-bulb temperature in the shade included: air temperature, location (ground vs canopy), plant species (*Boscia albitrunca*, *Senegalia mellifera* or *Vachellia erioloba*), the interaction between air temperature and location and the interaction between air temperature and plant species. The global model for black-bulb temperature in the sun included air temperature, location (ground vs above-ground), placement (*Boscia albitrunca*, *Senegalia mellifera*, *Vachellia erioloba*, dead tree or open ground), the interaction between air temperature and location and the interaction between air temperature and placement.

All box and whisker plots in the results show the median value with lower and upper quartiles and minimum and maximum values.

Results

Exploring individual relationships between explanatory variables, air temperature and FID

All models in this section are general linear mixed models (random term transect identity) investigating the potential relationships between explanatory variables (air temperature, microsite selection and bird activity) and FID, as well as between the variables (microsite selection and bird activity) and air temperature, one variable at a time. All models of FID also include starting distance as a co-variate.

The relationship between air temperature and FID

The air temperatures at which flight initiation distances were measured for the eight focal bird species ranged from 11.9 ^{o}C to 40.4 ^{o}C (Appendix Table B1). Air temperature had a weak significant negative effect on flight initiation distance (FID) overall for the eight focal bird species (t = -2.30; n = 633; Figure 4). There was an estimated 0.15 m decrease in FID for each 1 ^{o}C rise in air temperature (95% CI: -0.3 – -0.02 m).

In separate models, using subsets of the air temperature data, air temperature of 35 ^{o}C and above did not have a significant effect on FID overall for the eight focal bird species (t = -0.63; n = 137) nor did air temperature less than 35 ^{o}C have a significant effect on FID overall for the eight focal bird species (t = -1.82; n = 496).

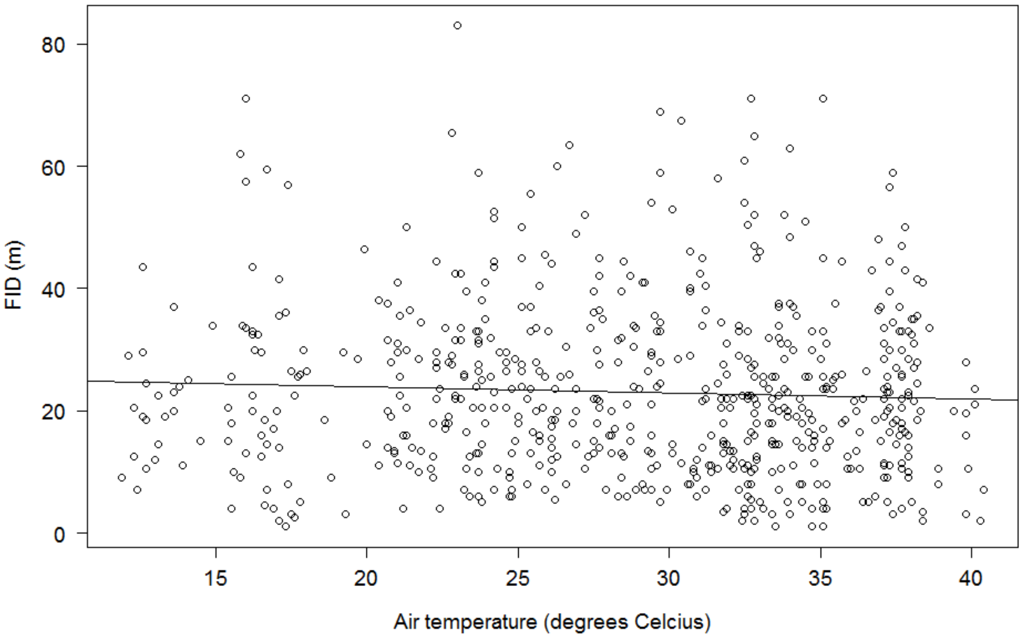

Figure 4: The weak significant negative effect of air temperature on the overall flight initiation distance (FID) of eight focal bird species (n = 633) in the Kalahari Desert during October and November 2015.

Exploring indirect effects of air temperature on FID via effects on behaviour

Indirect mechanisms through which air temperature may affect FID were investigated by examining the relationships between FID and behavioural variables (related to microsite selection: plant species selected, bird location, bird exposure; plus the activity of the bird prior to approach, i.e. stationary vs mobile); and the potential links between these behavioural variables and air temperature (relationships summarised in Figure 5, and detailed below).

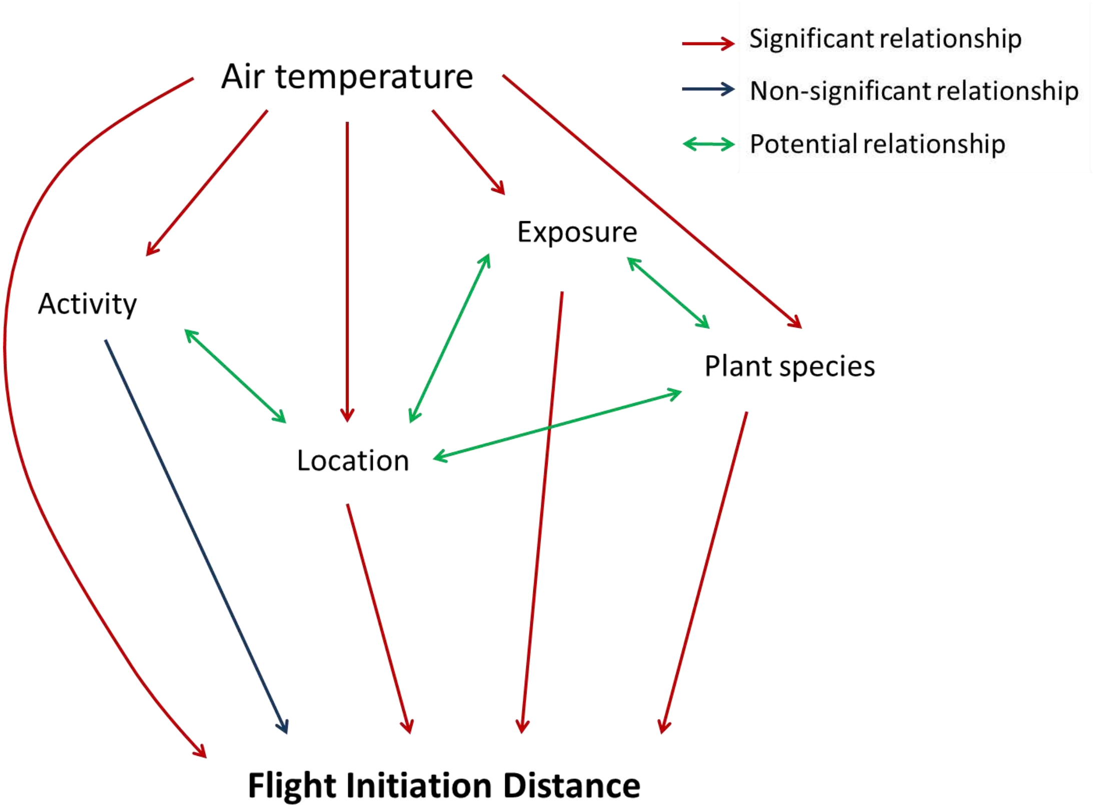

Figure 5: There was a significant negative relationship between air temperature and FID (-0.15 m/^{o}C). Air temperature was also found to have an effect on bird activity (mobile vs stationary), location (tree top vs canopy or ground), exposure (in the sun vs in the shade) and the plant species used by the birds. Of these, a difference in location, exposure and plant species were found to affect FID, as outlined in the text below. Potential relationships (in green) were not examined statistically.

Plant species

There were significant differences in the FID of birds when flushed from different plants (Figure 6 and Appendix Table D1). Mean FID from *Boscia albitrunca* (n = 104) was significantly shorter than from *Vachellia erioloba* by 4.1 m (95% CI: 0.5 – 7.7 m; n = 230) and from dead trees by 9.4 m (95% CI: 2.1 – 16.6 m; n = 21). Mean FID from *Senegalia mellifera* (n = 196) was significantly shorter than from *Vachellia erioloba* by 4.7 m (95% CI: 1.7 – 7.6 m), from dead trees by 10 m (95% CI: 3 – 16.9 m) and from *Rhigozum trichotomum* by 8.6 m (95% CI: 0.9 – 16.2 m; n = 17).

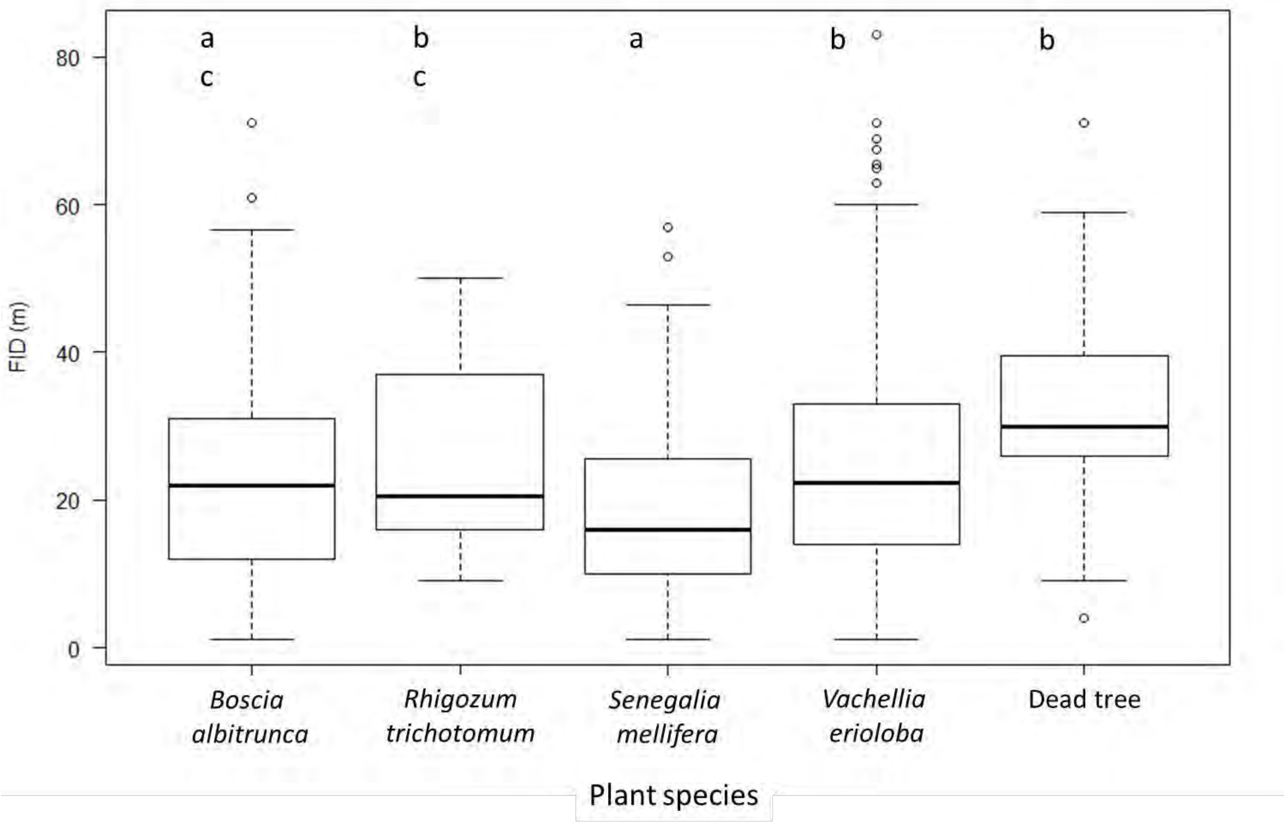

Figure 6: Box and whisker plot of the FIDs recorded for eight focal bird species in five plant species (*Boscia albitrunca* n = 104, *Rhigozum trichotomum* n = 17, *Senegalia mellifera* n = 196, *Vachellia erioloba* n = 230 and dead tree n = 21) in the Kalahari Desert during October and November 2015.

There was no significant difference in mean air temperature between the observations of the eight focal bird species in different plant species, except for a significantly higher (4.7 ^{o}C, 95% CI: 0.3 – 9.2 ^{o}C) mean air temperature for observations of birds in/under *Vachellia erioloba* compared to *Rhigozum trichotomum* (Figure 7 and Appendix Table D2).

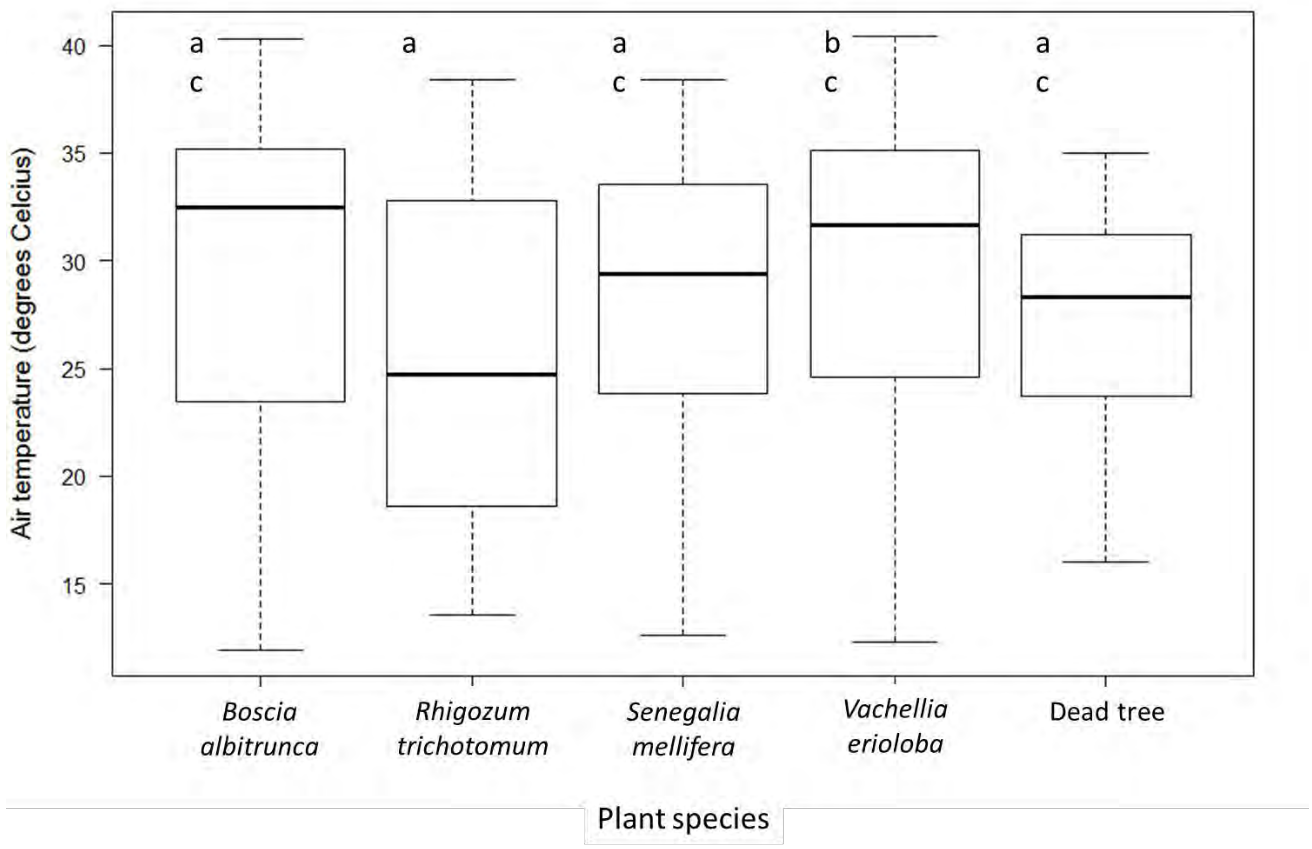

Figure 7: The relationship between plant species used by the eight focal bird species in this study and the air temperature at which these plants were used. (*Boscia albitrunca* n = 104, *Rhigozum trichotomum* n = 17, *Senegalia mellifera* n = 196, *Vachellia erioloba* n =230, dead tree n = 21).

Bird exposure

FIDs of birds in the sun (n = 157) were on average 3.5 m longer than FIDs of birds in the shade (n = 315; t = 3.36; 95% CI: 1.4 – 5.5 m; Figure 8).

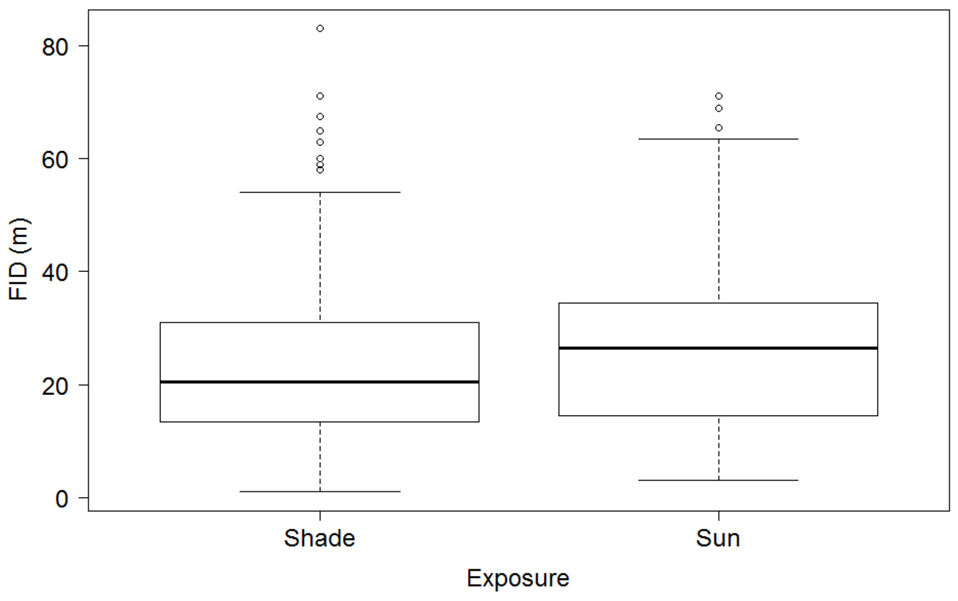

Figure 8: Box and whisker plot of the flight initiation distance (FID) for eight focal bird species located in the shade or in the sun in the Kalahari Desert during October and November 2015 (shade n = 315, sun n = 157). FIDs of birds in the shade were significantly shorter than birds in the sun (t = 3.36).

The eight focal bird species were observed in the sun at significantly cooler air temperatures than when observed in the shade (difference of 4.7 ^{o}C, 95% CI: 3.5 – 5.9 ^{o}C; t = -7.54; Figure 9).

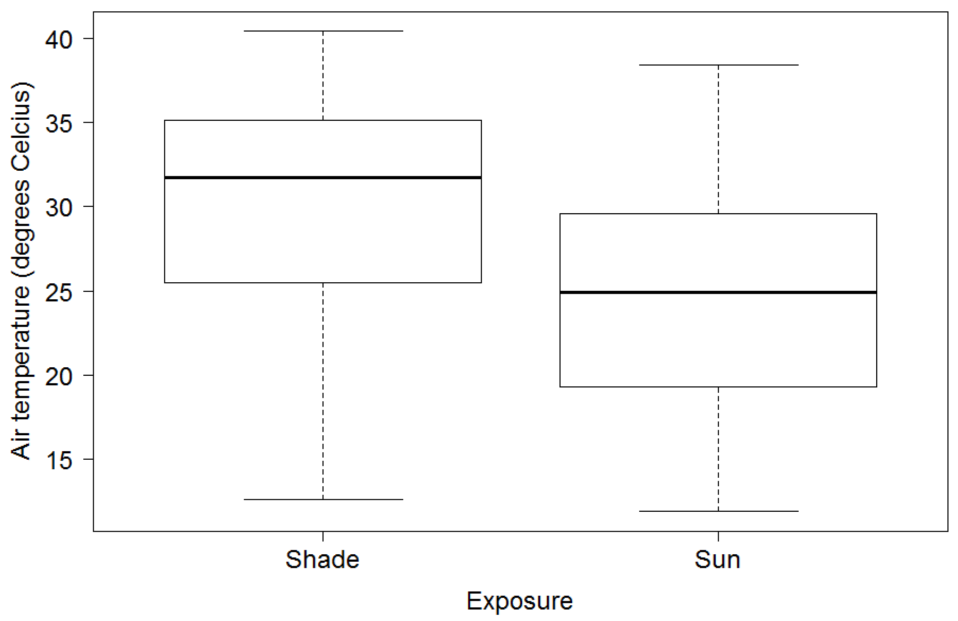

Figure 9: Box and whisker plot of the air temperature at which eight focal bird species were observed in the shade and in the sun in the Kalahari Desert in October and November 2015. (Shade n = 315, Sun n = 157). Birds were observed in the shade at significantly higher air temperatures than birds in the sun (t = -7.54).

Bird location

Mean FID was significantly shorter when birds were located in the canopy of a tree (n = 349) compared to if they were located on the ground (by 7.1 m, 95% CI: 4.5 – 9.8 m; n = 174), at the top of the tree (by 6.7 m, 95% CI: 3.2 – 10.2 m; n = 79) or in a dead tree (by 11.5 m, 95% CI: 4.2 – 18.8 m; n = 15); however there were no significant differences in FID between ground, tree top and dead tree locations (Figure 10 and Appendix Table D3).

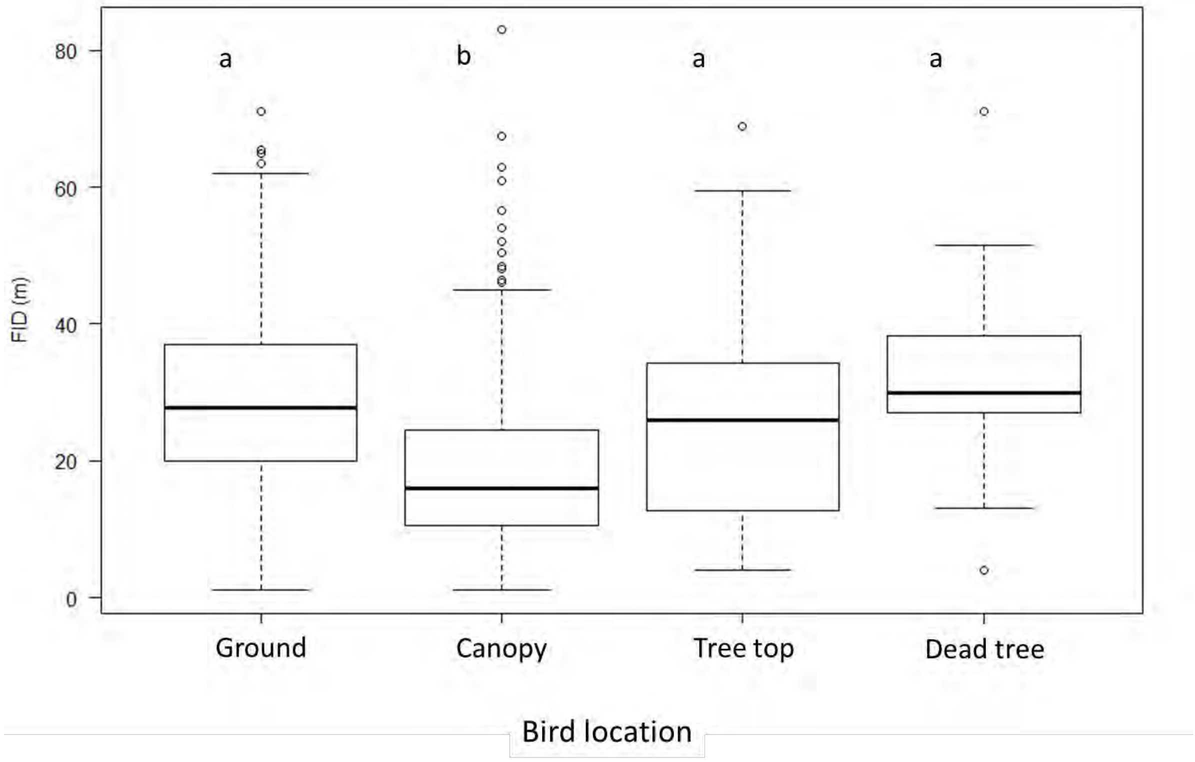

Figure 10: Box and whisker plot of the flight initiation distance (FID) for eight focal bird species in different locations in the Kalahari Desert during October and November 2015 (ground n = 174, canopy n = 349, tree top n = 79, dead tree n = 15).

There were no significant differences in air temperature between observations of birds on the ground, in the canopy of a tree, or in dead trees. However, birds were observed on tree tops at significantly lower air temperatures than when they were observed within the canopy (difference of 3.6 ^{o}C, 95% CI: 1.5 – 5.7 ^{o}C) or on the ground (difference of 3.4 ^{o}C, 95% CI: 1.1 – 5.6 ^{o}C; Figure 11 and Appendix Table D4).

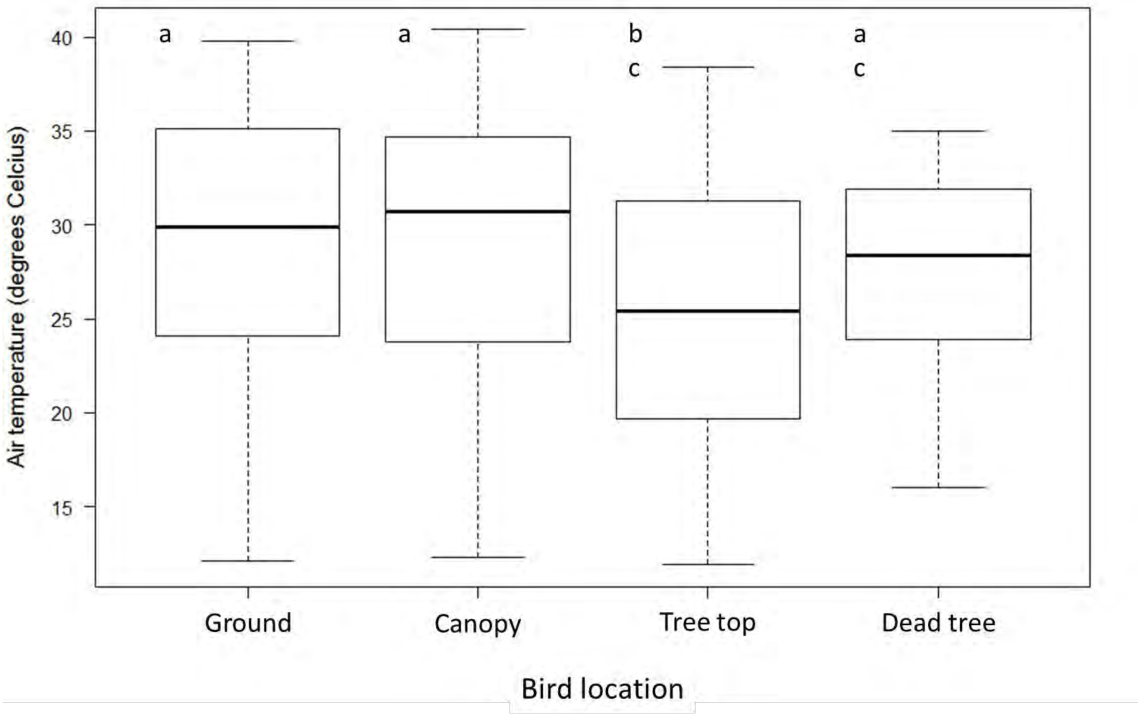

Figure 11: Box and whisker plot of the air temperature at which eight focal bird species used different locations in the Kalahari Desert in October and November 2015. (Ground n = 174, Canopy n = 349, Tree top n = 79, Dead tree n = 15).

Bird activity

There was no significant difference in FID between mobile (n = 270) and stationary birds (n = 202; t = 1.39), despite a tendency for stationary birds to have longer FIDs (Figure 12).

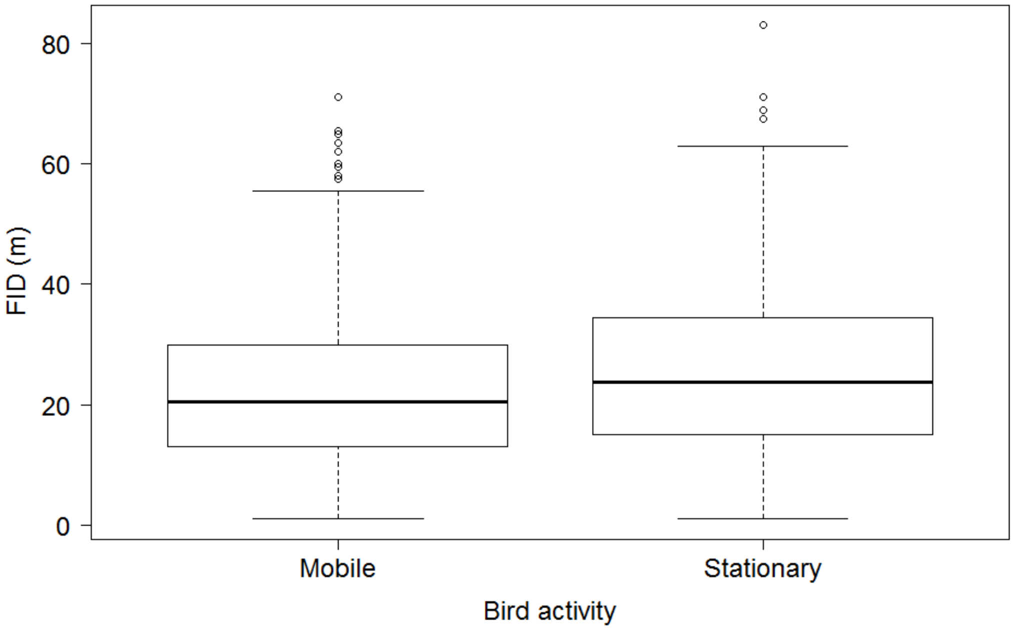

Figure 12: Box and whisker plot of the flight initiation distance (FID) for mobile (n = 270) and stationary (n = 202) birds of eight focal species in the Kalahari Desert during October and November 2015.

There was a weak significant difference in mean air temperature between observations of mobile and stationary birds in this study (t = 2.09). Observations of stationary birds occurred at air temperatures on average 1.3 ^{o}C (95% CI: 0.08 – 2.5 ^{o}C) higher than for mobile birds (Figure 13).

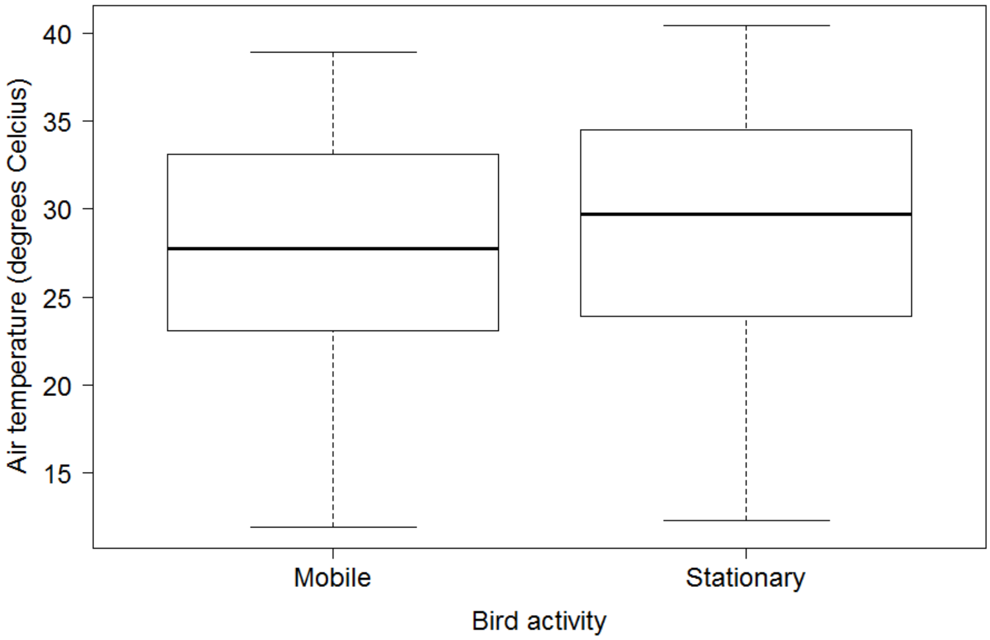

Figure 13: Box and whisker plot of the air temperature at which mobile and stationary birds of eight focal species were observed in the Kalahari Desert in October and November 2015. (Mobile n = 270, Stationary n = 202).

Comparison with hot (35 °C and higher) and cool (below 35 °C) air temperature data subsets

While air temperature was found to have significant relationships with FID and the four behavioural (three microsite and one activity-related) variables tested when looking at the full range of air temperatures (Figure 5), no significant relationships with air temperature were found in the subset of temperatures of 35 °C and higher (perhaps due to reduced sample size; n = 137 observations; Figure 14). In the subset of temperatures below 35 °C, bird exposure and bird location were found to have significant relationships with air temperature, but FID, bird activity and plant species selected did not (n = 496 observations; Figure 15). The three microsite selection variables (plant species, exposure and location) were found to have an effect on FID when looking at the full range of air temperatures and the subset of temperatures below 35 °C (Figures 5 and 15 respectively). At air temperatures of 35 °C and higher, plant species and bird location were found to affect FID (exposure was not analysed as there were only eight observations in the sun, compared to 85 observations in the shade in this data subset; Figure 14).

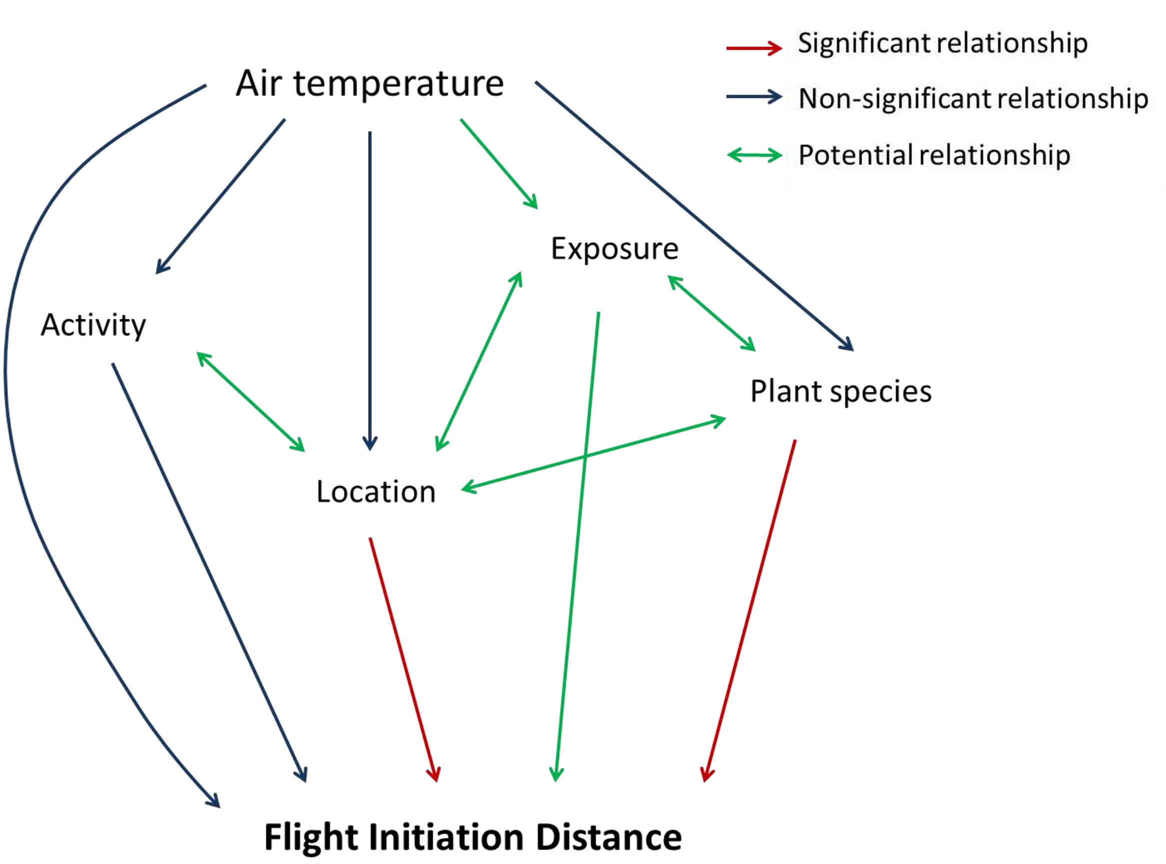

Figure 14: A summary of the relationships between air temperature, behavioural variables and FID at air temperatures of 35 °C and higher. Air temperature was not found to have a significant effect on FID or the three behavioural variables tested (exposure was not analysed as there were only eight observations in the sun, compared to 85 observations in the shade in this data subset). A difference in bird location ($\mathrm{FID}_{\mathrm{ground}} > \mathrm{FID}_{\mathrm{canopy}}$) and plant species ($\mathrm{FID}_{\textit{Boscia albitrunca}} > \mathrm{FID}_{\textit{Senegalia mellifera}}$; $\mathrm{FID}_{\textit{Vachellia erioloba}} > \mathrm{FID}_{\textit{Senegalia mellifera}}$) were found to affect FID at temperatures of 35 °C and higher. Potential relationships (in green) were not examined statistically.

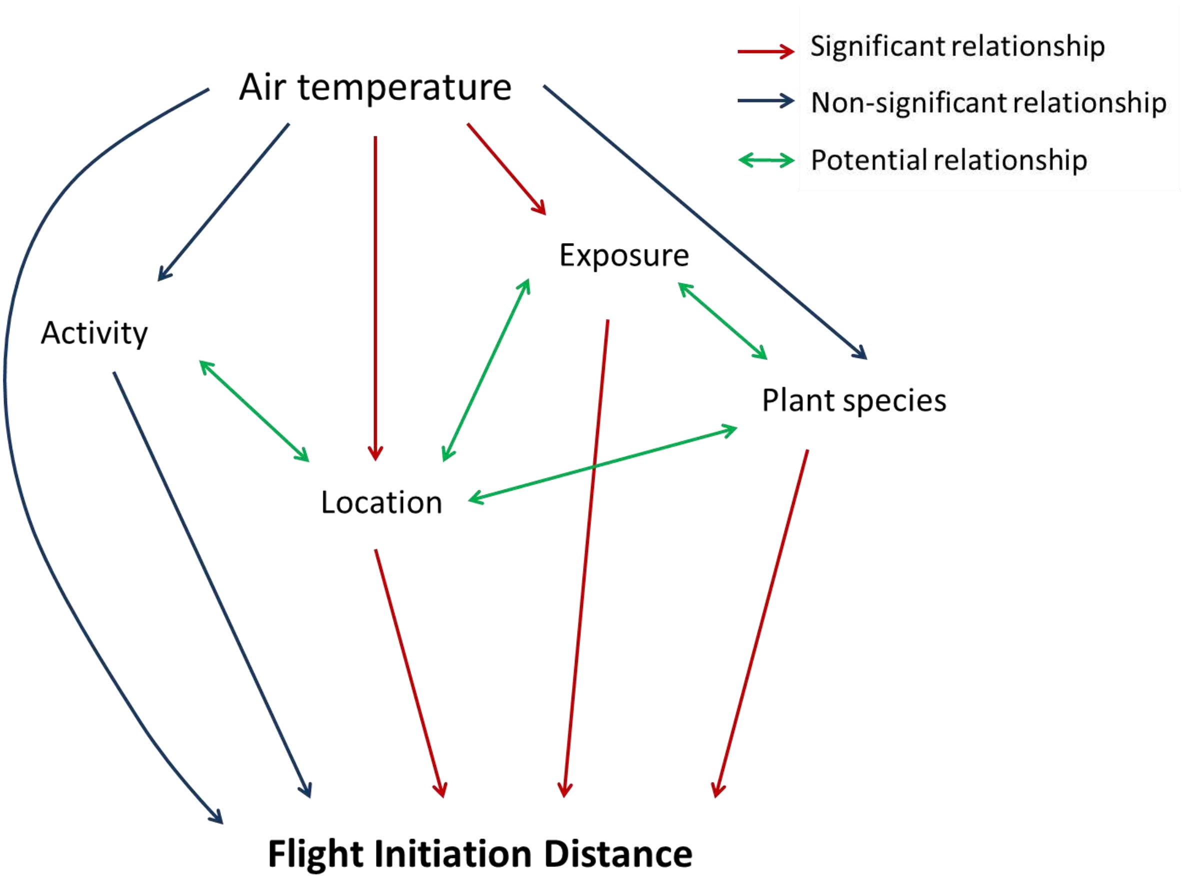

Figure 15: A summary of the relationships between air temperature, behavioural variables and FID at air temperatures below 35 ^{o}C. Air temperature was not found to have a significant effect on FID or on the plant species birds selected or whether birds were mobile or stationary at air temperatures below 35 ^{o}C. In this data subset, however, birds were observed in the shade and in the sun (exposure) at significantly different temperatures ($T_{a(shade)} > T_{a(sun)}$), and in different locations at different temperatures ($T_{a(canopy)} > T_{a(tree\ top)}$). Exposure ($FID_{sun} > FID_{shade}$), location ($FID_{ground} > FID_{canopy}$, $FID_{tree\ top} > FID_{canopy}$, $FID_{dead\ tree} > FID_{canopy}$) and plant species ($FID_{Vachellia\ erioloba} > FID_{Senegalia\ mellifera}$, $FID_{dead\ tree} > FID_{Senegalia\ mellifera}$, $FID_{dead\ tree} > FID_{Boscia\ albitrunca}$) were found to affect FID at temperatures below 35 ^{o}C. Potential relationships (in green) were not examined statistically.

The relationships between air temperature and the four behavioural variables, as well as between the behavioural variables and their impact on FID were found to differ between bird species. Three examples of individual bird species analysis (Scaly-feathered Finch, Fawn-coloured Lark and Cape Turtle Dove) are given in Appendix C.

Full model analyses: the role of air temperature together with other factors affecting FID

In this section, top models (delta AICc < 2) were selected from nested model sets drawn from global models that included other possible drivers of FID that I measured in the field. This was to investigate the relationship between air temperature and FID accounting for the influence of other important variables.

Factors explaining variation in FID across the full range of air temperatures observed

The global model fitted to investigate factors influencing FID across all observed air temperatures included air temperature, starting distance, time of day, bird species, plant species, bird location, bird exposure and bird activity, with a random term for transect. From the set of all possible nested models, four were within 2 AICc points of the best-fit model (Table 1). Air temperature was not selected in any of these models, but starting distance, bird species and all microsite variables (plant species, location and exposure) were selected in all four models. Time of day and bird activity were each selected in two of the top four models.

Table 1: The explanatory variables selected in the top models (delta AICc < 2) of flight initiation distance (m) for eight focal bird species as a group, across all recorded temperatures in the Kalahari Desert in October and November 2015.

Model	**T_a**	**Starting distance**	**Time of day**	**Bird species**	**Plant species**	**Location**	**Exposure**	**Activity**	**df**	**AICc**	**delta**	**weight**
1		0.49	✓	✓	✓	✓	✓	✓	23	3435.1	0.00	0.277
2		0.49		✓	✓	✓	✓	✓	21	3435.7	0.56	0.209
3		0.49	✓	✓	✓	✓	✓		22	3436.1	0.96	0.171
4		0.49		✓	✓	✓	✓		20	3436.7	1.63	0.123

Global model: air temperature + starting distance + time of day + bird species + plant species + location + exposure + activity. Random term: transect. N = 467. ✓ = selected in the model.

Starting distance

Starting distance was selected in each of the top four models explaining FID when looking across the full range of air temperatures (Table 1). There was a significant, positive relationship between starting distance and FID. In the best-fit model from Table 1, FID increased by 0.49 m (95% CI: 0.43 – 0.55 m) for each 1 m increase in starting distance (t = 15.42; Table 2).

Time of day

Time of day was selected in two of the top four models explaining FID (Table 1). Although it was selected in the best-fit model, the models where it was not selected were less than two AICc units higher. Despite its apparent importance in explaining some of the variation in FID there were no significant differences in FID between the different times of day in the best-fit model explaining FID (Model 1 in Table 1; see Appendix Table D5 for multiple comparisons of means).

Bird species

Bird species was selected in each of the top four models explaining FID when looking at the full range of air temperatures (Table 1). There were significant differences in FID between bird species (Figure 16 and Appendix Table D6) in the best-fit model (Model 1 in Table 1). Cape Turtle Doves (n = 58) have the largest average body mass (130.3 g) of the eight species and had significantly longer mean FID than two of the four species with lowest mass in the group: 9.3 m longer than Black-chested Prinia (95% CI: 2 – 16.6 m; n = 63; mass = 8.9 g) and 10.6 m longer than Chestnut-vented Tit-Babbler (95% CI: 3.4 – 17.8 m; n = 56; mass = 15.7 g). Chestnut-vented Tit-Babbler also had a significantly shorter mean FID than Kalahari Scrub-Robin (7.2 m, 95% CI: 0.2 – 14.2 m; n = 44; mass = 19.7 g).

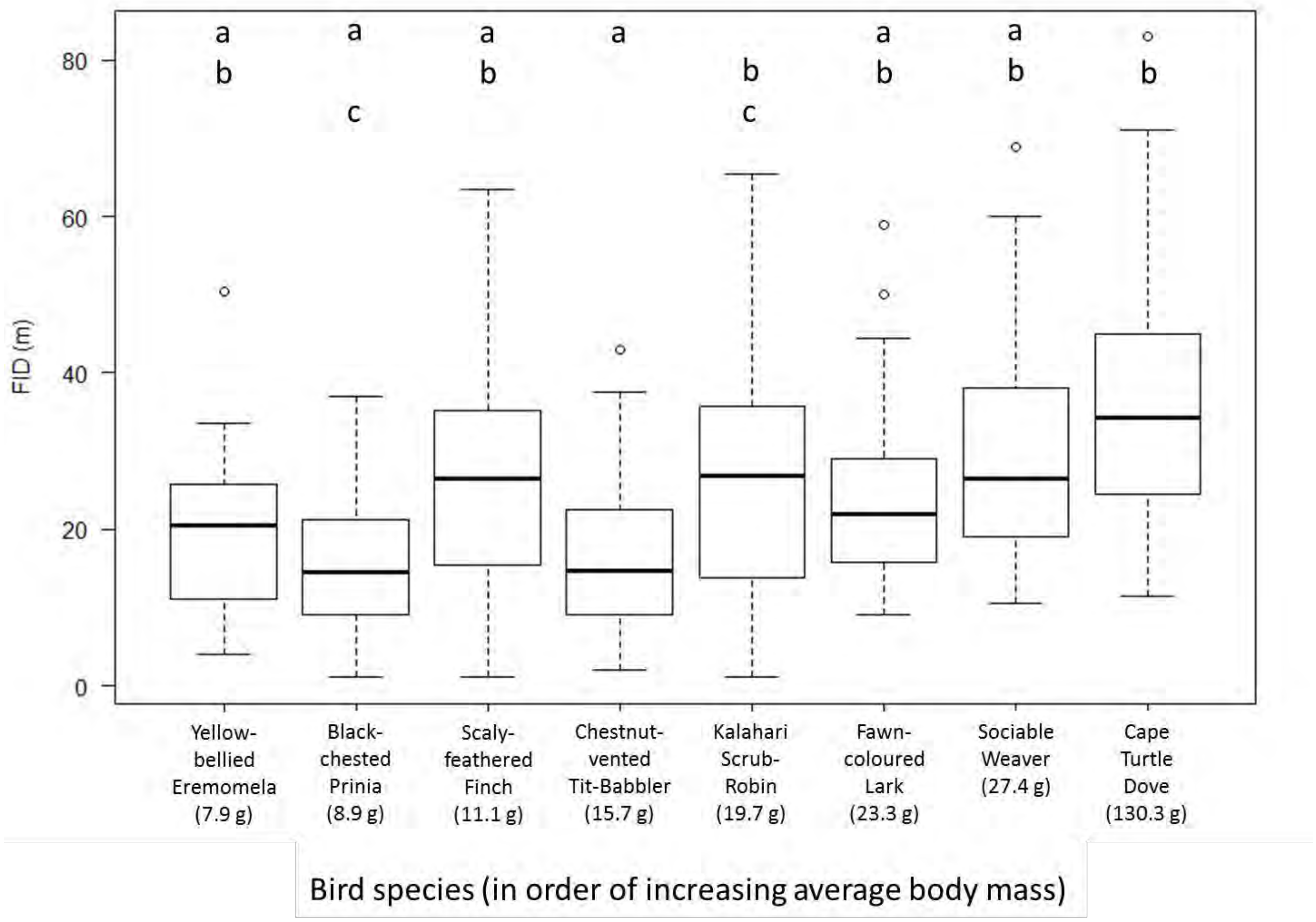

Figure 16: Box and whisker plot of the flight initiation distance (FID) of eight bird species (Yellow-bellied Eremomela n = 47, Black-chested Prinia n = 63, Scaly-feathered Finch n = 95, Chestnut-vented Tit-Babbler n = 56, Kalahari Scrub-Robin n = 44, Fawn-coloured Lark n = 63, Sociable Weaver n = 41 and Cape Turtle Dove n = 58) in the Kalahari Desert from October and November 2015. (Body mass data from Hockey *et al*. 2005).

Plant species

The plant species in/under which the birds were observed, was selected in all top four models explaining FID when looking at the full range of air temperatures (Table 1). There was a significant difference in the FID of birds flushed from *Vachellia erioloba* compared to birds flushed from *Senegalia mellifera* in the top model from Table 1 (Appendix Table D7). Mean FID of birds flushed from *Senegalia mellifera* (n = 152) was 4.7 m shorter than from *Vachellia erioloba* (95% CI: 1.5 – 7.9m; n = 185).

Bird location

Location (whether the bird was on the ground, in the canopy of a tree, on the top of a tree or in a dead tree) was selected in all top four models explaining FID when looking at the full range of air temperatures (Table 1). Despite its apparent importance in explaining some of the variation in FID there were no significant differences in FID between birds in the different locations in the best-fit model explaining FID (Model 1 in Table 1; see Appendix Table D8 for multiple comparisons of means).

Bird exposure

Exposure (whether the bird was in the shade or in the sun when the approach began) was selected in all top four models explaining FID when looking at the full range of air temperatures (Table 1). FIDs of birds in the sun (n = 154) were on average 2.5 m longer than FIDs of birds in the shade (n = 313) in the best-fit model of FID (Table 2), however, this difference was not significant (t = 1.74).

Bird activity

Activity (whether the bird was mobile or stationary when the approach began) was selected in two of the top four models explaining FID when looking at all temperatures as a whole (Table 1). Although it was selected in the best-fit and second top models, the models where it was not selected were less than two AICc units different from these. There was no significant difference in FID between mobile (n = 267) and stationary birds in the best-fit model (t = -0.82; n = 200; Table 2)

Table 2: A summary of the effect of each explanatory variable on FID (m), based on the best-fit model (Model 1 in Table 1) of FID with observations across all temperatures. This model includes starting distance, plant species (reference variable: no plant, i.e. open ground), bird species (reference variable: Black-chested Prinia), time of day (reference variable: afternoon), activity (reference variable: mobile), exposure (reference variable: shade) and location (reference variable: canopy).

Variable	**Estimate**	**Std. Error**	**t value**
Intercept	-2.06	2.76	-0.746
Starting distance	0.49	0.03	15.421
Plant species: *Boscia albitrunca*	0.65	2.25	0.287
Plant species: Dead tree	-1.01	4.72	-0.214
Plant species: *Rhigozum trichotomum*	4.71	3.26	1.448
Plant species: *Senegalia mellifera*	-2.72	2.05	-1.331
Plant species: *Vachellia erioloba*	1.95	2.08	0.936
Bird species: Cape Turtle Dove	9.30	2.42	3.84
Bird species: Chestnut-vented Tit-Babbler	-1.29	1.89	-0.683

Bird species: Fawn-coloured Lark	3.48	2.46	1.413
Bird species: Kalahari Scrub-Robin	5.90	2.25	2.618
Bird species: Scaly-feathered Finch	4.75	2.02	2.355
Bird species: Sociable Weaver	5.57	2.38	2.343
Bird species: Yellow-bellied Eremomela	1.99	1.97	1.011
Time of day: Early morning	0.95	1.24	0.764
Time of day: Late morning	0.92	1.09	0.845
Activity: Stationary	-1.14	1.40	-0.82
Exposure: Sun	2.50	1.44	1.735
Location: Dead tree	10.30	5.31	1.938
Location: Ground	3.07	1.72	1.789
Location: Tree top	2.66	1.80	1.477

Factors explaining variation in FID at hot (> 35 °C) and cool (< 35 °C) air temperatures

Hot air temperatures (> 35 °C)

There was a clearly best model to explain FID at air temperatures of 35 °C and higher (all others were > 2 AICc points away). This model contained air temperature, starting distance, time of day, bird species, plant species, bird location and bird activity (n = 84; Tables 3 and 4). Exposure was not included as a variable in the global model for FID at temperatures of 35 °C and above as there were only two observations in the sun, compared to 82 observations in the shade in this dataset.

Table 3: The explanatory variables selected in the best-fit model (delta AICc < 2) of flight initiation distance (m) for eight focal bird species when air temperature was equal to, or above, 35 °C in the Kalahari Desert in October and November 2015. Bird exposure was not included in this model as there were only two observations of birds in the sun in this dataset.

Model	T_a	Starting distance	Time of day	Bird species	Plant species	Location	Activity	df	AICc	weight
1	-2.52	0.36	✓	✓	✓	✓	✓	17	577	0.619

Global model: air temperature + starting distance + time of day + bird species + plant species + location + activity.
Random term: transect. N = 84. ✓ = selected in the model.

Air temperature explained a significant portion of the variation in FID at air temperatures of 35 °C and higher, once the variation due to starting distance, time of day, bird species, microsite (plant species and location) and activity was accounted for by including these variables in the model. FID decreased by an estimated 2.5 m (95% CI: -4.8 – 0.02 m) per 1 °C rise in air temperature (t = -2.13; Table 4). Starting distance once again had a significant positive relationship with FID, where FID increased by an estimated 0.36 m with each 1 m increase in starting distance (95% CI: 0.2 – 0.5 m; t = 4.76; Table 4). There was also a significant effect of time of day. FIDs in the late morning when air temperatures were at or over 35 °C (n = 17) were on average 7.6m (95% CI: 1.2 – 14.9 m) shorter than in the afternoon at high air temperatures (no early morning observations exceeded an air temperature of 35 °C; t = -2.31; n = 67; Table 4).

At air temperatures of 35 °C and higher there were differences in FID between bird species: Kalahari Scrub-Robins (n = 8) had significantly longer FIDs than Black-chested Prinias (by 16.9 m; 95% CI: 3.6 – 30.2 m; n= 8) and Sociable Weavers (by 15.9 m, 95% CI = 1.2 – 30.6 m; n = 6; Appendix Table D9).

With regard to the behavioural variables, birds in / under *Vachellia erioloba* trees (n = 48) had significantly longer FIDs than birds in / under *Boscia albitrunca* (by an average of 6.9 m, 95% CI: 0.3 – 13.5 m, n = 16) and *Senegalia mellifera* (by an average of 12.2 m, 95% CI: 6.1 – 18.3 m; n = 20; Appendix Table D10). There was no significant difference in FID between birds in / under *Boscia albitrunca* and those in / under *Senegalia mellifera* at temperatures of 35 °C and above (t = -1.61; Table 4). FIDs of birds on the ground (n = 33) were significantly longer than when birds were in the canopy of a tree in this dataset (an average difference of 8.3 m, 95% CI: 2.3 – 14.3 m; t = 2.70; n = 51; Table 4). There was no significant difference in FID between mobile (n = 44) and stationary birds at air temperatures of 35 °C and above (t = -1.47; n = 40; Table 4).

Table 4: A summary of the effect of each explanatory variable on FID (m), based on the best-fit model (Table 3) of FID with observations at air temperatures at or above 35 °C. This model includes starting distance, plant species (reference variable: *Boscia albitrunca*), bird species (reference variable: Black-chested Prinia), air temperature, time of day (reference variable: afternoon), activity (reference variable: mobile) and location (reference variable: canopy).

Variable	**Estimate**	**Std. Error**	**t value**
Intercept	92.59	43.99	2.105
Starting distance	0.36	0.08	4.759
Plant species: *Senegalia mellifera*	-5.30	3.30	-1.607
Plant species: *Vachellia erioloba*	6.90	2.81	2.459
Bird species: Cape Turtle Dove	11.50	5.07	2.266
Bird species: Chestnut-vented Tit-Babbler	3.83	4.04	0.948
Bird species: Fawn-coloured Lark	3.59	5.36	0.67
Bird species: Kalahari Scrub-Robin	16.89	4.43	3.81
Bird species: Scaly-feathered Finch	8.18	4.03	2.029
Bird species: Sociable Weaver	1.02	5.04	0.203
Bird species: Yellow-bellied Eremomela	3.01	4.94	0.61
Air temperature	-2.52	1.18	-2.127
Time of day: Late morning	-7.63	3.31	-2.308
Activity: Stationary	-3.72	2.54	-1.466
Location: Ground	8.29	3.07	2.703

Cool air temperatures (< 35 ^{o}C)

Two top models were chosen to explain FID at air temperatures cooler than 35 ^{o}C (all others were > 2 AICc points away; n = 374; Table 5). Neither of these models contained air temperature, but both models contained starting distance, time of day, bird species, plant species, bird location and bird exposure. Bird activity was selected in the best-fit model explaining FID at temperatures below 35 ^{o}C but not in the second top model, less than one AICc unit higher (Table 5).

Table 5: The explanatory variables selected in the top models (delta AICc < 2) of flight initiation distance (m) for eight focal bird species when air temperature was below 35 ^{o}C in the Kalahari Desert in October and November 2015.

Model	**T_a**	**Starting distance**	**Time of day**	**Bird species**	**Plant species**	**Location**	**Exposure**	**Activity**	**df**	**AICc**	**delta**	**weight**
1		0.50	✓	✓	✓	✓	✓	✓	23	2746.4	0.00	0.376
2		0.50	✓	✓	✓	✓	✓		22	2747.3	0.88	0.242

Global model: air temperature + starting distance + time of day + bird species + plant species + location + exposure + activity. Random term: transect. N = 374. ✓ = selected in the model.

FID had a significant positive relationship with starting distance, increasing by 0.5 m (95% CI: 0.4 – 0.6 m) with each 1 m increase in starting distance in Model 1 in Table 5 (t = 14.36; Table 6). There were no significant differences in FID between the different times of day in this dataset (in Model 1, Table 5; early morning n = 130, late morning n = 144, afternoon n = 100; Appendix Table D11).

There were significant differences in FID between some bird species at temperatures below 35 ^{o}C (from Model 1 in Table 5). Chestnut-vented Tit-Babblers (n = 46) had significantly shorter mean FIDs than Cape Turtle Doves (by 11 m, 95% CI: 2.6 – 19.4 m; n = 44) and Sociable Weavers (by 8.7 m, 95% CI: 0.2 – 17.1 m; n = 34; Appendix Table D12). Cape Turtle Dove had a close to significantly longer mean FID than Black-chested Prinia (a difference of 8.5 m, 95% CI: -0.004 - 17 m; n = 55; Appendix Table D12).

Looking at the behavioural variables in Model 1 in Table 5, there was a significant difference in mean FID between birds flushed from *Vachellia erioloba* (n = 136) and *Senegalia mellifera* (n = 130). FID for birds in / under *Vachellia erioloba* was on average 3.7 m (95% CI: 0.06 – 7.2 m) longer than for birds in / under *Senegalia mellifera* (Appendix Table D13). There were however, no significant differences in FID between birds flushed from different locations (Appendix Table D14), or between birds in the sun and in the shade (t = 1.68; Table 6). There was also no difference between the FIDs of mobile and stationary birds in this dataset (t = -0.50; Table 6).

Table 6: A summary of the effect of each explanatory variable on FID (m), based on the best-fit model (Model 1 in Table 5) of FID with observations at air temperatures below 35 ^{o}C. This model includes starting distance, plant species (reference variable: no plant, i.e. open ground), bird species (reference variable: Black-chested Prinia), time of day (reference variable: afternoon), activity (reference variable: mobile), exposure (reference variable: shade) and location (reference variable: canopy).

Variable	**Estimate**	**Std. Error**	**t value**
Intercept	-2.42	3.10	-0.783
Starting distance	0.50	0.04	14.363
Plant species: *Boscia albitrunca*	-0.38	2.54	-0.151
Plant species: Dead tree	-1.37	4.84	-0.283
Plant species: *Rhigozum trichotomum*	4.15	3.45	1.204
Plant species: *Senegalia mellifera*	-2.58	2.26	-1.141
Plant species: *Vachellia erioloba*	1.08	2.27	0.474
Bird species: Cape Turtle Dove	8.49	2.82	3.008
Bird species: Chestnut-vented Tit-Babbler	-2.50	2.10	-1.193
Bird species: Fawn-coloured Lark	3.26	2.82	1.158
Bird species: Kalahari Scrub-Robin	3.95	2.59	1.529
Bird species: Scaly-feathered Finch	4.59	2.38	1.926
Bird species: Sociable Weaver	6.15	2.75	2.241
Bird species: Yellow-bellied Eremomela	1.54	2.13	0.721
Time of day: Early morning	1.55	1.40	1.103
Time of day: Late morning	2.32	1.35	1.722
Activity: Stationary	-0.85	1.71	-0.496
Exposure: Sun	2.53	1.51	1.68
Location: Dead tree	11.03	5.44	2.028
Location: Ground	2.50	2.10	1.19
Location: Tree top	1.61	1.87	0.859

Species-specific models of the factors affecting FID

These models were fitted across all air temperatures as there were not enough data to examine hot and cool temperatures separately. (The number of FID measurements at hot temperatures for each species is given in Appendix B). Air temperature was not selected in any of the top models explaining FID individually for the eight focal species. Starting distance was selected in all top models explaining FID for seven of the eight focal bird species (Table 7). Starting distance was not selected in the best-fit model of FID for Yellow-bellied Eremomela. Its addition in the second top model for this species increased AICc by 0.2 units. Time of day was selected in all top models explaining FID individually for the eight focal bird species (Table 7).

Of the variables describing microsite choice of the bird, plant species was selected in all models in the top model set (delta AICc < 2) for all species (Table 7). Bird location was also selected in all top models (where there were sufficient data in at least two location categories to include this variable into the models), except in the third top model for Kalahari Scrub-Robin (Table 7). Exposure was selected in all the best-fit models explaining FID individually for the eight focal bird species (where there were sufficient data of both sun and shade categories to include this variable into the models; Table 7). However, for four of the seven species where exposure was included in the global model, this variable was not selected in all of the models in the top model set (delta AICc < 2), i.e. it was not selected in the second top models for Black-chested Prinia, Kalahari Scrub-Robin and Sociable Weaver or the third top model for Fawn-coloured Lark (Table 7).

Bird activity was also selected in all models in the top model set (delta AICc < 2) explaining FID individually for the eight focal bird species (where there were sufficient data in both activity categories to include this variable in the models), except in the second top model for Fawn-coloured Lark and the third top model for Sociable Weaver (Table 7).

Model output tables for the best-fit model for each bird species, including effect sizes and test statistics, are presented in Appendix E.

Table 7: The explanatory variables selected in the top models (delta AICc < 2) that explain flight initiation distance (m) individually for eight bird species in the Kalahari Desert in October and November 2015. (✓ = selected for the model; not included = not added to the model, due to insufficient data).

Species	n	No. of best models	T_a	Starting distance	Time of day	Plant species	Location	Exposure	Activity	df	AICc	delta	weight
Black-chested Prinia	60	2		0.30	✓	✓	✓	✓	not included	10	408.0	0.00	0.329
				0.29	✓	✓	✓		not included	9	408.9	0.84	0.216
Cape Turtle Dove	50	1		0.71	✓	✓	✓	✓	✓	11	374.7	0.00	0.334
Chestnut-vented Tit-Babbler	54	1		0.32	✓	✓	not included	not included	not included	8	381.0	0.00	0.667
Fawn-coloured Lark	53	3		0.45	✓	✓	✓	✓	✓	12	359.0	0.00	0.316
				0.47	✓	✓	✓	✓		11	360.7	1.69	0.136
				0.45	✓	✓	✓		✓	11	360.9	1.89	0.123
Kalahari Scrub-Robin	38	3		0.58	✓	✓	✓	✓	✓	11	274.7	0.00	0.311
				0.59	✓	✓	✓		✓	10	276.4	1.76	0.129
				0.56	✓	✓		✓	✓	10	276.5	1.85	0.123
Scaly-feathered Finch	93	1		0.46	✓	✓	✓	✓	✓	14	680.6	0.00	0.434
Sociable Weaver	40	3		0.54	✓	✓	✓	✓	✓	13	276.5	0.00	0.309
				0.54	✓	✓	✓		✓	12	277.5	0.97	0.190
				0.53	✓	✓	✓	✓		12	277.6	1.02	0.185
Yellow-bellied Eremomela	47	2			✓	✓	✓	✓	not included	9	327.5	0.00	0.312
				0.25	✓	✓	✓	✓	not included	10	327.7	0.20	0.282

Global model: air temperature + starting distance + time of day + plant species + location + exposure + activity, except where some of these variables were not included due to too few data, as indicated in the table. Random term: transect.

Comparing black-bulb temperatures in different locations and plant species; and assessing interactions between these variables and air temperature

In the shade

Exploring the effects of location and plant species independently of air temperature

In a linear model of black-bulb temperature in the shade there was a significant difference between black-bulb temperature on the ground versus in the canopy of a tree / bush (Figure 17). Mean black-bulb temperature in the shade on the ground was 1.4 ^{o}C (95% CI: 1.1 – 1.8 ^{o}C) higher than in the shade in the canopy of the three plant species used (t = 8.75, p < 0.001).

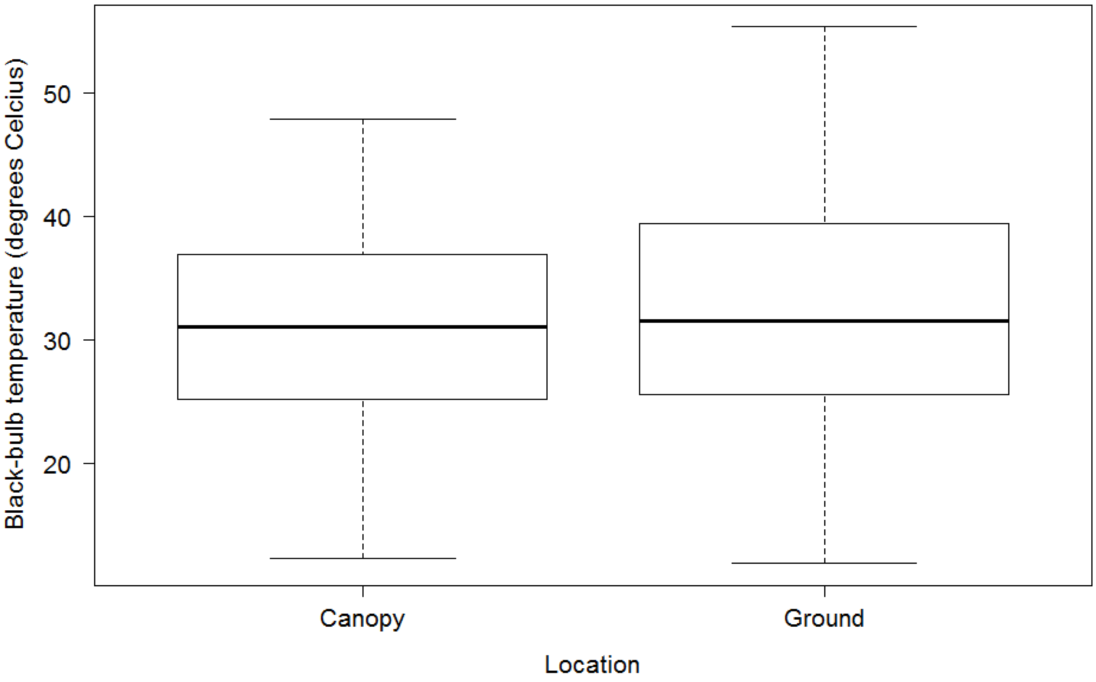

Figure 17: Black-bulb temperature in the shade in the canopy and on the ground below three plant species (*Boscia albitrunca*, *Senegalia mellifera*, *Vachellia erioloba*) from data measured in the early morning (07:00 – 09:00), late morning (10: - 12:00) and afternoon (14:00 – 16:00) in the Kalahari Desert in October and November 2015.

There were also significant differences between the black-bulb temperatures in the shade of different plant species (Figure 18 and Appendix Table D15). Mean black-bulb temperature in the shade of *Senegalia mellifera* was higher than in the shade of *Boscia albitrunca* by 2.8 ^{o}C (95% CI: 2.4 – 3.3 ^{o}C) and higher than in the shade of *Vachellia erioloba* by 1.9 ^{o}C (95% CI: 1.4 – 2.3 ^{o}C). Mean black-bulb temperature in the shade of *Vachellia erioloba* was higher than in the shade of *Boscia albitrunca* by 0.96 °C (95% CI: 0.5 – 1.4 °C).

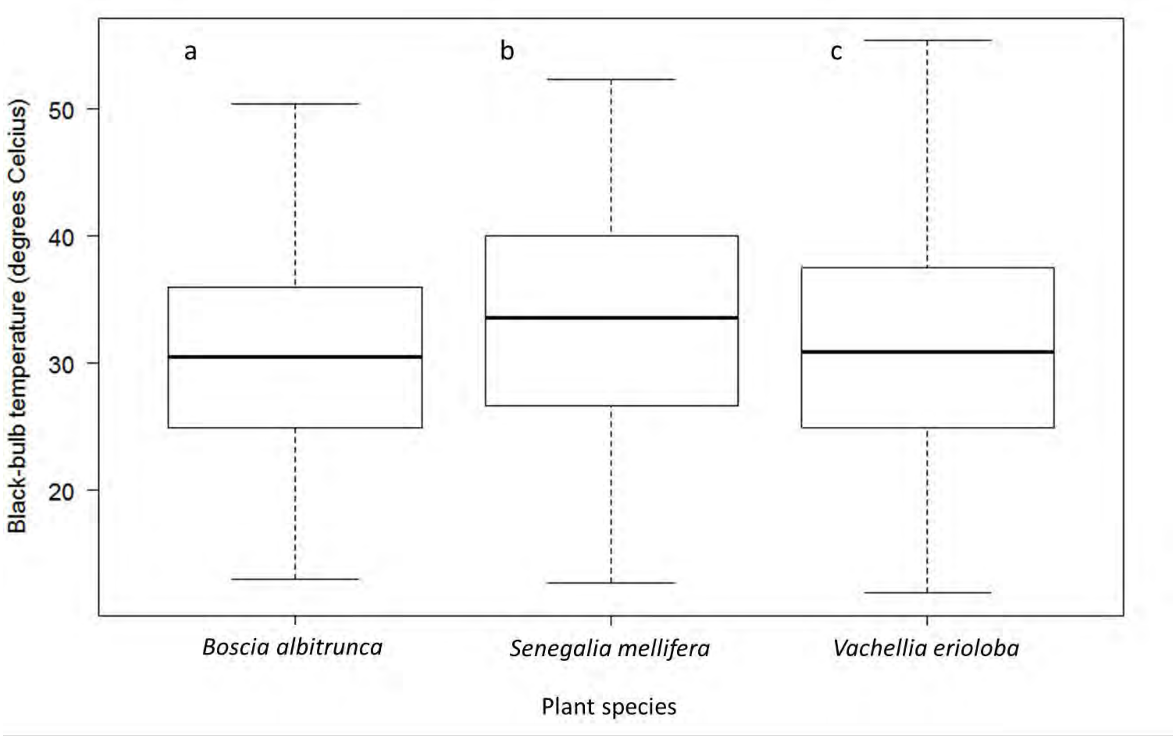

Figure 18: The difference in black-bulb temperature in the shade of different plant species from data measured in the early morning (07:00 – 09:00), late morning (10: - 12:00) and afternoon (14:00 – 16:00) in the Kalahari Desert in October and November 2015.

Modelling how the effects of air temperature on black-bulb temperature are influenced by location and plant species

In the global model of black-bulb temperature in the shade, (a linear model that included air temperature, location (ground vs canopy), plant species (*Boscia albitrunca*, *Senegalia mellifera*, *Vachellia erioloba*) and the interactions of air temperature with these variables), there was only one best-fit model with delta AICc < 2 (Tables 8 and 9). All variables in the global model were selected in this model.

Table 8: The explanatory variables selected in the best-fit model (delta AICc < 2) of black-bulb temperature (°C) in the shade in the Kalahari Desert in October and November 2015.

Model	**T_a**	**Location**	**Plant species**	**Ta*Location**	**Ta* Plant species**	**df**	**AICc**	**delta**	**weight**
1	0.97	✓	✓	✓	✓	9	45499.5	0.00	1

Global model: air temperature + location + plant species + air temperature*location + air temperature*plant species.
✓ = selected in the model.

Table 9: A summary of the effect of each explanatory variable on black-bulb temperature (^{o}C) in the shade, based on the best-fit model (Table 8). This model includes air temperature, plant species (reference variable: *Boscia albitrunca*), Location (reference variable: Canopy), the interaction between air temperature and plant species (reference variable: *Boscia albitrunca*) and the interaction between air temperature and location (reference variable: Canopy).

Variable	**Estimate**	**Std. Error**	**t value**	**Pr(>|t|)**	**Significance code**
Intercept	2.40	0.18	13.287	< 0.001	***
Air temperature	0.97	0.01	154.412	< 0.001	***
Plant species: *Senegalia mellifera*	-0.22	0.22	-0.999	0.318	
Plant species: *Vachellia erioloba*	-2.50	0.22	-11.262	< 0.001	***
Location: Ground	-2.45	0.18	-13.56	< 0.001	***
Air temperature*Plant species: *Senegalia mellifera*	0.11	0.01	14.766	< 0.001	***
Air temperature*Plant species: *Vachellia erioloba*	0.12	0.01	16.08	< 0.001	***
Air temperature* Location: Ground	0.14	0.01	22.213	< 0.001	***

Significance codes: *** < 0.001; ** < 0.01; * < 0.05; . < 0.1

In shaded locations, the temperature recorded by black-bulbs placed on the ground increased faster with air temperature than the temperature recorded by black-bulbs placed in the canopies of plants (Figure 19 and Table 9). There were also significant differences in the relationship between black-bulb temperature in the shade and air temperature between plant species. The temperature of black-bulbs placed in the shade within or under *Senegalia mellifera* increased faster with increasing air temperature than those placed in the shade within or under *Boscia albitrunca*. Likewise, the temperature of black-bulbs placed in the shade within or under *Vachellia erioloba* increased more rapidly with air temperature than those associated with *Boscia albitrunca* (Figure 20 and Table 9).

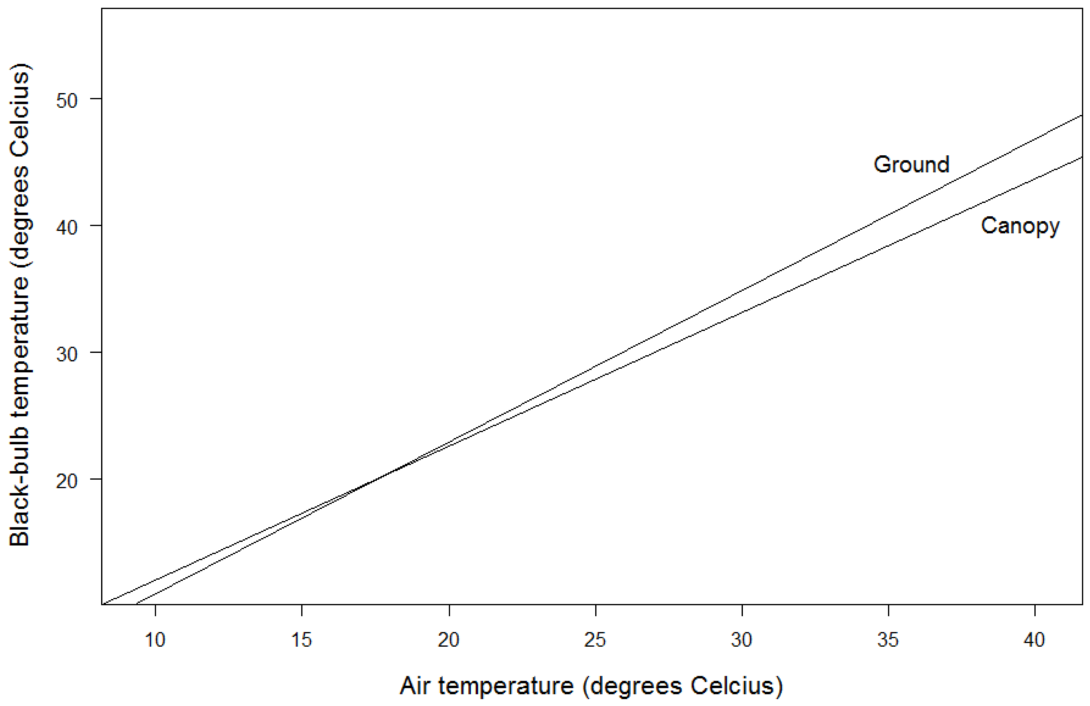

Figure 19: The relationship between air temperature and black-bulb temperature in the shade on the ground compared to in the canopy of three plant species (*Boscia albitrunca*, *Senegalia mellifera*, *Vachellia erioloba*) from data measured in the early morning (07:00 – 09:00), late morning (10: - 12:00) and afternoon (14:00 – 16:00) in the Kalahari Desert in October and November 2015.

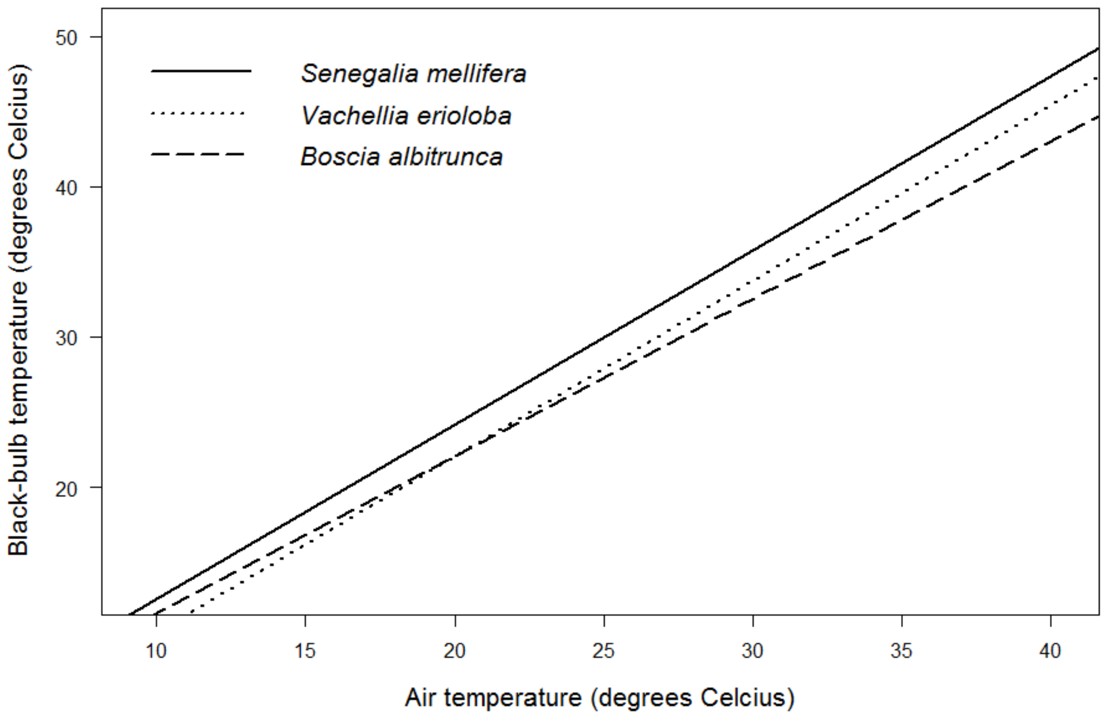

Figure 20: The relationship between air temperature and black-bulb temperature in the shade of three plant species from data measured in the early morning (07:00 – 09:00), late morning (10: - 12:00) and afternoon (14:00 – 16:00) in the Kalahari Desert in October and November 2015.

In the sun

Exploring the effect of placement independently of air temperature

In a linear model of black-bulb temperature in the sun there were significant differences between placements (i.e. between different tree species, dead trees and open ground; Figure 21 and Appendix Table D16). Mean black-bulb temperature in the sun on the ground was significantly higher than in each of the above-ground placements in the sun (a difference of 3 ^{o}C, 95% CI: 2.2 – 3.8^{o}C, compared with *Boscia albitrunca;* 3.8 ^{o}C, 95% CI: 3 – 4.6 ^{o}C, compared with *Senegalia mellifera*; 5.5 ^{o}C, 95% CI: 4.7 – 6.3 ^{o}C, compared with *Vachellia erioloba* and 5.8 ^{o}C, 95% CI: 5 – 6.6 ^{o}C, compared with dead trees). Mean black-bulb temperature in the sun was lowest in dead trees, 2.8 ^{o}C (95% CI: 2 – 3.5 ^{o}C) lower than *Boscia albitrunca*, 1.96 ^{o}C (95% CI: 1.2 – 2.8 ^{o}C) lower than *Senegalia mellifera* but not significantly different from *Vachellia erioloba*. Mean black-bulb temperature in the sun on *Boscia albitrunca* was close to significantly higher than on *Senegalia mellifera* ($p = 0.05$) and 2.5 ^{o}C (95% CI: 1.7 – 3.3 ^{o}C) higher than on *Vachellia erioloba*. Mean black-bulb temperature in the sun on *Senegalia mellifera* was 1.7 ^{o}C (95% CI: 0.9 – 2.5 ^{o}C) higher than on *Vachellia erioloba*.

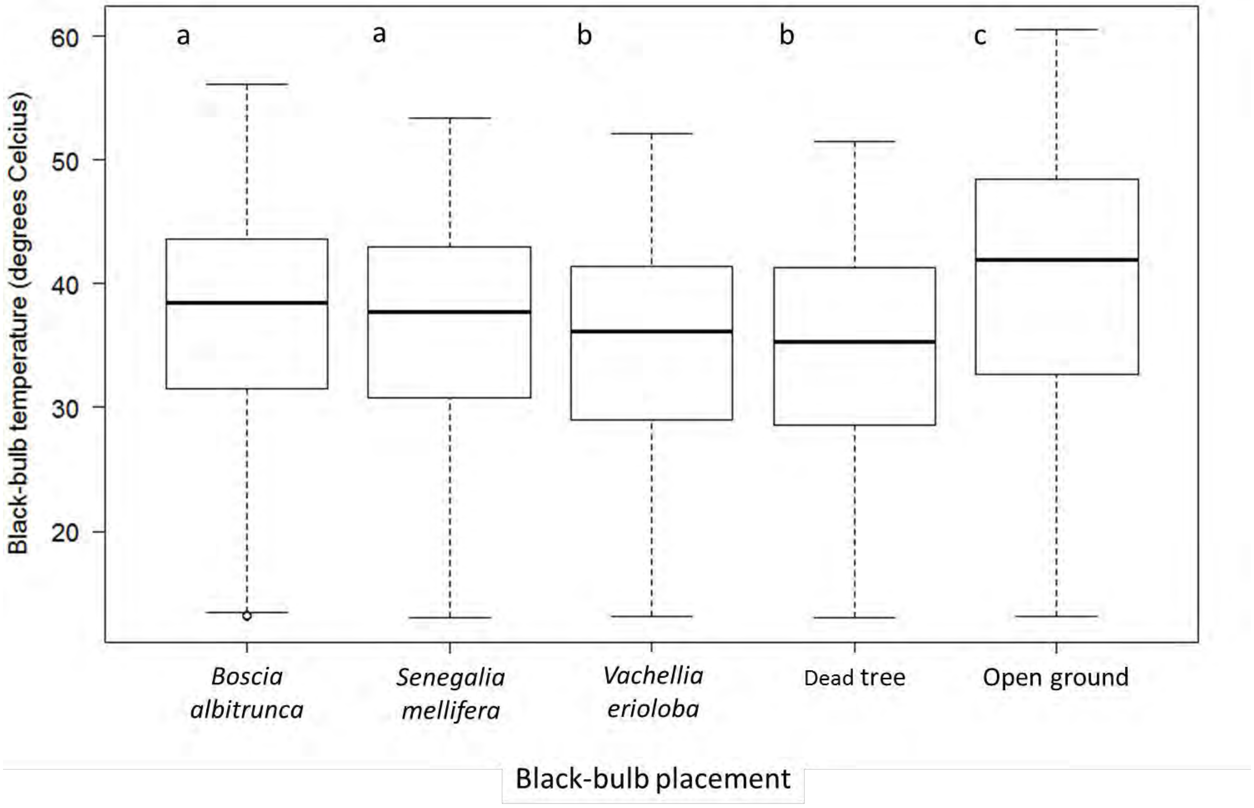

Figure 21: The difference in black-bulb temperature in different placements in the sun from data measured in the early morning (07:00 – 09:00), late morning (10: - 12:00) and afternoon (14:00 – 16:00) in the Kalahari Desert in October and November 2015.

Modelling how the effects of air temperature on black-bulb temperature are influenced by location and placement

In the global model of black-bulb temperature in the sun, (a linear model that included air temperature, location (ground vs above-ground), placement (*Boscia albitrunca*, *Senegalia mellifera*, *Vachellia erioloba*, dead tree or open ground) and the interactions of air temperature with these variables), there were three models with delta AICc < 2, all with identical AICc values (Tables 10 and 11). The variable: location (ground vs above-ground) was not selected in any of these three top models without placement being included in the model. This highlighted the importance of the differences between the above-ground placements in describing black-bulb temperature in the sun. Air temperature, placement and the interaction between air temperature and placement were selected in all three top models.

Table 10: The explanatory variables selected in the best-fit models (delta AICc < 2) of black-bulb temperature (^{o}C) in the sun in the Kalahari Desert in October and November 2015. (Location refers to ground vs above-ground and placement refers to *Boscia albitrunca* vs *Senegalia mellifera* vs *Vachellia erioloba* vs dead tree vs open ground).

Model	**T_a**	**Location**	**Placement**	**Ta*Location**	**Ta* Placement**	**df**	**AICc**	**delta**	**weight**
1	1.01		✓		✓	11	44128.6	0.00	0.333
2	1.01	✓	✓		✓	11	44128.6	0.00	0.333
3	1.01	✓	✓	✓	✓	11	44128.6	0.00	0.333

Global model: air temperature + location + placement + air temperature*location + air temperature*placement.
✓ = selected in the model.

Table 11: A summary of the effect of each explanatory variable on black-bulb temperature (^{o}C) in the sun, based on the best-fit model (Model 1 in Table 10) with the least number of variables (three models each had the same AICc values). This model includes air temperature, placement (reference variable: *Boscia albitrunca*) and the interaction between air temperature and placement (reference variable: *Boscia albitrunca*).

Variable	**Estimate**	**Std. Error**	**t value**	**Pr(>|t|)**	**Significance code**
Intercept	9.24	0.32	28.906	< 0.001	***
Air temperature	1.01	0.01	90.511	< 0.001	***
Placement: Dead tree	-5.27	0.45	-11.674	< 0.001	***
Placement: Open ground	-5.57	0.45	-12.34	< 0.001	***
Placement: *Senegalia mellifera*	-1.62	0.45	-3.6	< 0.001	***
Placement: *Vachellia erioloba*	-4.47	0.45	-9.881	< 0.001	***
Air temperature*Placement: Dead tree	0.09	0.02	6.008	< 0.001	***
Air temperature*Placement: Open ground	0.31	0.02	19.951	< 0.001	***
Air temperature*Placement: *Senegalia mellifera*	0.03	0.02	2.144	0.032	*
Air temperature*Placement: *Vachellia erioloba*	0.07	0.02	4.569	< 0.001	***

Significance codes: *** < 0.001; ** < 0.01; * < 0.05; . < 0.1

There were significant differences in the relationship between black-bulb temperature in the sun and air temperature when looking at the different placements. Compared to *Boscia albitrunca*, the positive relationship between black-bulb temperature in the sun and air temperature was steeper on *Senegalia mellifera*, *Vachellia erioloba*, dead trees and open ground (Figure 22 and Table 11). However, the strongest effect was open ground, where black-bulb temperatures increased more rapidly with air temperature than any of the off-ground locations (Figure 22 and Table 11).

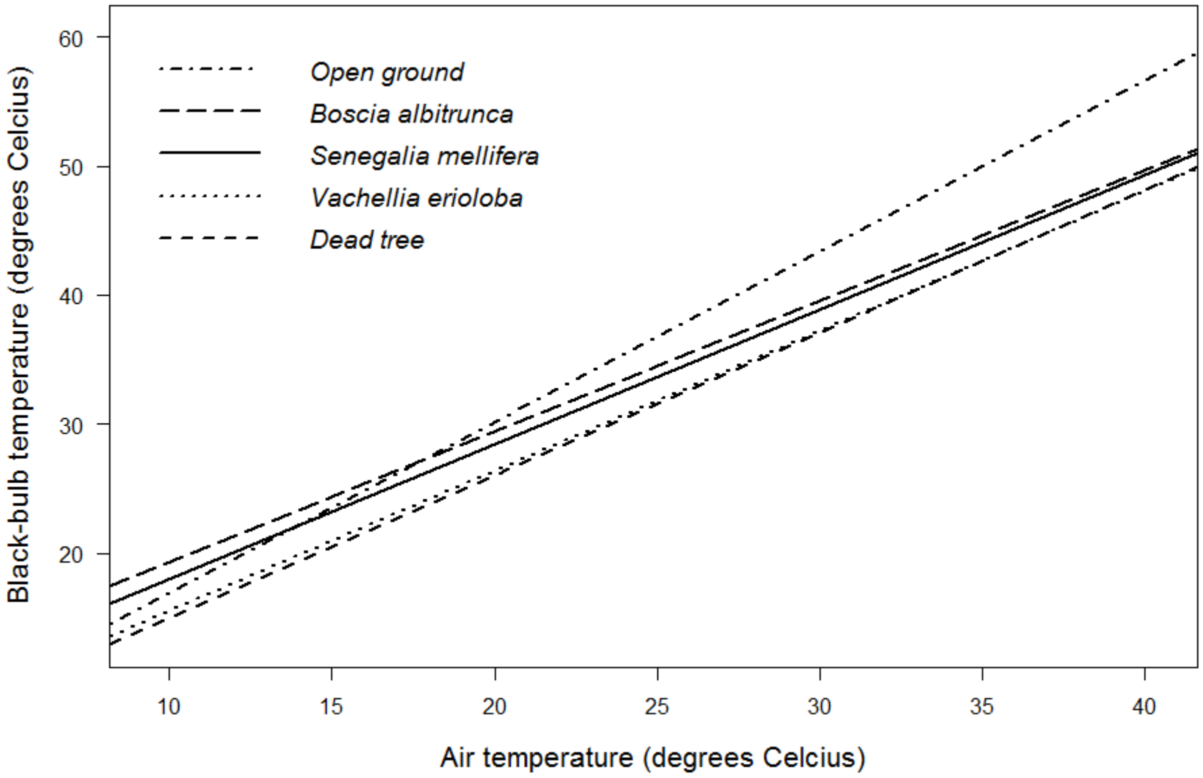

Figure 22: The relationship between air temperature and black-bulb temperature in different placements in the sun from data measured in the early morning (07:00 – 09:00), late morning (10: - 12:00) and afternoon (14:00 – 16:00) in the Kalahari Desert in October and November 2015.

Discussion

The aim of this study was to determine whether differences in air temperature have an effect on anti-predator behaviour in arid-zone birds, with a view to understanding one aspect of how predation risk might change for birds in the Kalahari under climate change. I predicted that FID would decrease with increasing air temperature due to the increased thermoregulatory cost of fleeing at high temperatures. Looking at the full range of air temperatures observed during the study period I found that as air temperature increased, FID did indeed decrease significantly. However, this relationship was weak, with a large amount of variability in FID not explained by air temperature. Air temperature was not selected to explain variation in the models of FID below 35 ^{o}C and across the full range of air temperatures observed. In these models, other explanatory variables such as starting distance, time of day, bird species, microsite selection and bird activity were selected. In the model of FID at temperatures of 35 ^{o}C and higher, these explanatory variables were also selected to account for variation in FID, but air temperature became a significant factor too, accounting for an average decrease in FID of 2.5 m per 1 ^{o}C rise in air temperature. In the single variable analysis of FID and air temperatures of 35 ^{o}C and higher (with starting distance as co-variate), there was no significant relationship between air temperature and FID. However, once variation attributable to time of day, bird species, plant species, bird location and bird activity had been accounted for, the significant effect of air temperature became apparent. This indicates that high air temperature, together with other explanatory variables are important in explaining the variation in FID observed in my study.

Fleeing generates metabolic heat together with potentially exposing the birds to higher environmental temperatures if they are fleeing from a cooler microsite (e.g. fleeing from the shade of a tree and being exposed to increased solar radiation in the sun). This poses thermoregulatory challenges to birds when air temperatures are high, particularly for arid-zone birds, as it may cause their body temperatures to approach lethal limits and water scarcity makes evaporative cooling costly. Smit (2013) studied the heat dissipation behaviour (panting / gular fluttering) of birds in the Kalahari. The HD_{start} values (estimated as the air temperature at which the probability of heat dissipation exceeds 5%) for the eight focal bird species in my study range from 33 ^{o}C (for Fawn-coloured Lark) to 36.2 ^{o}C (for Scaly-feathered Finch) (Smit 2013). Air temperature thus appears to become a constraining factor for the birds in my study from the mid-30s upwards. Because of the thermoregulatory challenges birds face at high temperatures they are likely to be more reluctant to flee, resulting in what is seen in my results as a substantial decrease in FID as temperatures rise above 35 ^{o}C. Lower air temperatures will pose fewer thermoregulatory challenges to the birds and is likely why air temperature had much less of an effect on FID in my data at lower temperatures (less than 35 °C).

The influence of other variables on FID

Bird species

Blumstein *et al*. (2003) found FID to be a species-specific trait for shorebirds in Australia. In my study, bird species was consistently selected in the models using high temperatures, cool temperatures and the full range of temperatures, to explain some of the variation in FID, with some significant differences in FID between species. Blumstein (2006) and Guay *et al*. (2013) also found a relationship between bird body size and FID; birds with larger mass having longer FIDs. In all cases where significant differences in FID were found between bird species in my data, the bird with the larger average body mass had the longer FID of the two species, except in one case in the subset of data at high (35 °C and above) air temperatures, where Kalahari Scrub-Robin (average body mass = 19.7 g) had a significantly longer mean FID than Sociable Weaver (average body mass = 27.4 g; body mass data from Hockey *et al*. 2005).

Behavioural differences between bird species in terms of their reaction to our approach were noticeable in the field. Cape Turtle Doves for example seemed to be a lot warier of our approach towards them than other species were, on many occasions flying away before we had seen them in the distance. These observations are reflected in the results, with Cape Turtle Doves having significantly longer FIDs than some of the other species, e.g. longer than Chestnut-vented Tit-Babblers in the best-fit models across all temperatures, as well as cool temperatures, and longer FIDs than Black-chested Prinias across all temperatures (and close to significantly longer at cool temperatures). In the individual species models of FID, starting distance was also found to play a larger role in Cape Turtle Dove observations than for any other species. In the best-fit model of FID for Cape Turtle Doves, FID increased by an average 0.71 m per 1 m increase in starting distance, compared to all other species where FID increased by less than 0.6 m per 1 m increase in starting distance. Cape Turtle Doves thus appear to react earlier to an approach than other species. Cape Turtle Doves had the largest average body mass (130.3 g) of the eight focal species in this study (the next highest average body mass was 27.4 g for Sociable Weavers; Hockey *et al*. 2005). The positive relationship between body mass and flightiness in birds (Blumstein 2006 and Guay *et al*. 2013) discussed above may thus be contributing to the longer FIDs observed for Cape Turtle Doves in this study. Blumstein (2006) discusses a number of reasons why larger body size may result in longer FIDs, e.g. larger birds may be more vulnerable because they can be spotted by predators from a greater distance, or the possibility that larger species are less agile and therefore need to escape earlier, or that the cost of fleeing might be lower for larger birds because of relatively lower energy requirements than small birds and thus less need to risk remaining in order to continue foraging. I think it is likely that Cape Turtle Doves react earlier in the Kalahari because of being more vulnerable to predation as a result of being more visible to predators due to their larger size, less agile in their escape and also potentially because there are fewer options available to large birds compared to small birds in the Kalahari in terms of vegetation or shelter which they can escape to, due to the sparsity of suitable cover for large birds.

The factors influencing FID also differed between species. Although starting distance was consistently selected as being important in explaining variation in FID when analysing the eight focal species as a group, as well as for seven of the eight species individually, it was not important in the model of FID for Yellow-bellied Eremomela (where it was not selected to explain variation in the best-fit FID model for this species). The comparison of the relationships between separate behavioural variables and FID for three bird species in Appendix C, illustrates some differences too. For example, bird location and bird exposure were found to affect the FIDs of Scaly-feathered Finches, but not of Fawn-coloured Larks and Cape Turtle Doves. The plants the birds were in / under however, were found to affect FID for the latter two species, but not for Scaly-feathered Finches. My results highlight that not only are there differences in FID between species, but that the factors affecting FID differ between species.

Microsite selection variables – the impact of visibility, vulnerability and high temperatures

The three microsite selection variables (plant species, bird location and bird exposure) came out consistently in my results as being important in explaining FID. These three variables were selected in all models of FID looking at the eight focal species together (except in the model at high temperatures where exposure was not included due to insufficient observations in the sun) and in all best-fit models for the individual species, where there were sufficient data to include them.

I suggest that variation in the visibility of an approach, the degree of protection or shelter offered within the different levels of these variables and the thermal benefits of being in a particular microsite contribute to the effect of microsite selection on FID. With regards to plant species, FIDs of birds in or under *Senegalia mellifera* were significantly shorter than FIDs of birds in or under *Vachellia erioloba* in the best-fit models of FID looking at the full range of air temperatures, as well as at both high and cooler temperatures. These two plants differ in structure and likely in the protection offered from an approaching predator. *Senegalia mellifera* are bushes (with an average height of 1.8 m and width of 3.4 m for the FID measurements taken from this plant species in this study) with a dense network of thorn-covered branches. During the period over which the fieldwork for this study took place the majority of these bushes were without leaves.

Vachellia erioloba is more tree-like in structure than *Senegalia mellifera*, with fewer branches. While the *Vachellia erioloba* trees did have leaves during the study period they generally do not form a dense canopy in this species. The *Senegalia mellifera* bushes offer protection to birds within their canopy as these plants are virtually impenetrable to larger species or predators due to the dense network of branches and thorns. Birds on the ground below a *Senegalia mellifera* bush are also closer to the shelter or protection from the bush than those on the ground below *Vachellia erioloba*, as the canopy is often some metres above the birds when they are under a tree. I suggest that birds feel less vulnerable in or under *Senegalia mellifera* than in or under *Vachellia erioloba* and that this may be influencing the consistently shorter FIDs from *Senegalia mellifera* bushes than from *Vachellia erioloba* trees. It is worth mentioning here too that only three observations of Cape Turtle Doves were made on (the ground below) *Senegalia mellifera*, compared to 24 in or under *Vachellia erioloba* trees and, as discussed above, mean FID of Cape Turtle Doves was found to be significantly longer than for two other bird species in this study. The different bird species flushed from the two plants may thus also have contributed towards the difference in FID between these two plants. However, the single variable analysis of FIDs from different plant species supports the suggestion that the degree of shelter or protection offered may play a role in affecting FID. From the observations across all temperatures, mean FIDs of birds in or under *Senegalia mellifera* were not only shorter than *Vachellia erioloba*, but also shorter than for birds in dead trees or in or under *Rhigozum trichotomum* (a short shrub with an average height of 0.7 m and width of 0.9 m for observations in this study), neither of which offer as much shelter or protection as *Senegalia mellifera*. In the single variable analysis FIDs were also shorter from *Boscia albitrunca* than from dead trees or from *Vachellia erioloba*. *Boscia albitrunca* are trees with densely shaded canopies that are likely to provide more shelter or protection to a bird than *Vachellia erioloba* or a dead tree would, potentially contributing to the shorter FIDs from *Boscia albitrunca* trees.

Not only are *Boscia albitrunca* trees likely to offer birds more shelter or protection from predators, but the shade offered by these trees was found to be significantly cooler than the shade from *Senegalia mellifera* or *Vachellia erioloba*, as evidenced from the black-bulb thermometer analysis. From the best-fit model of FID at high temperatures, mean FID from *Boscia albitrunca* trees was significantly shorter than from *Vachellia erioloba* trees. The difference was not significant in the best-fit models at cool or overall temperatures. Birds thus appear to be delaying fleeing from *Boscia albitrunca* trees specifically at high temperatures, compared to *Vachellia erioloba*. This indicates a potential trade-off between predation risk and thermoregulation at high temperatures since my results indicate that birds are delaying fleeing (increased predation risk) for significantly longer from a cooler microsite (greater thermoregulatory benefits) at higher but not lower air temperatures. Hence, at high air temperatures, both the thermoregulatory benefits (shade from *Boscia albitrunca* is cooler than from *Vachellia erioloba*) and the greater protection offered by certain plants (birds in *Senegalia mellifera*, while hotter are likely to feel more sheltered or protected than in or under *Vachellia erioloba*) appear to be having an effect on reducing FID.

The important effect of the visibility of an approaching potential predator on FID is shown through the significant positive impact of starting distance on FID. Blumstein (2003) discusses that this may be due to the increased cost associated with having to monitor an approaching predator. Birds will thus fly sooner (longer FID) the earlier they are aware of an approaching predator so that they can reduce the cost of having to spend time watching and assessing the approaching threat. It is likely that the visibility of an approaching predator is greater for a bird on the top of a tree, in a dead tree or on the ground, compared to a bird in the canopy of a plant, due to the branches and / or leaves of a canopy obscuring the view. Birds are also potentially less vulnerable to predation from within the canopy of a plant compared to the other three locations due to the shelter or protection provided by the canopy. In my analysis, location (whether the bird was on the ground, in the canopy of a plant, on the top of a tree or in a dead tree) was consistently selected in the models to explain some of the variation in FID. Mean FIDs of birds from the canopies of plants were shorter than from the other locations in each of the best-fit models using the different temperature datasets. The reduced visibility of an approaching predator and vulnerability to predation might explain the shorter FIDs for birds in canopies compared to other locations and thus explain why location was consistently important in explaining variation in FID in my data.

However, although location was selected to explain variation in FID in all models, the differences between the different locations at cooler temperatures and looking across the full range of temperatures were not significant. At high temperatures though, FIDs of birds on the ground were significantly longer than birds in the canopy. Eighty-two of the eighty-four FID observations in this high temperature subset were in the shade and from the black-bulb temperature analysis my results show that black-bulb temperature on the ground in the shade was significantly higher than in the canopy shade of the three plant species tested. The significant difference between FIDs of birds in canopies and birds on the ground at high temperatures but not at cooler temperatures may point once again to a potential trade-off between predation risk and thermoregulation at high temperatures, since birds delay fleeing from the cooler microsite of a canopy for longer, relative to the ground, at high temperatures than cool temperatures.

The third microsite variable assessed was bird exposure. While this was not included in the models at high temperatures, it was selected in all models at cooler and the full range of temperatures to explain variation in FID. FIDs of birds in the sun were longer than FIDs of birds in the shade in all analyses. In order for birds to be in the sun, they need to be positioned in more open spaces, even within the canopy of a tree, without being shaded by a cover of branches or leaves. It is thus once again likely that in more open / less sheltered sites the birds had greater ability to see an approaching predator than birds in shaded microsites. Visibility may therefore also be impacting the influence of bird exposure on FID.

Although visibility appears to play an important role in influencing FID, it seems to play less of a role at high temperatures. In the best-fit model of FID at cooler temperatures the increase in FID was 0.5 m per 1 m increase in starting distance. At air temperatures of 35 ^{o}C and above, FID increased by an average of 0.36 m per 1 m increase in starting distance. At higher temperatures the observational cost associated with monitoring an approaching predator may thus be relatively lower. The reduced cost may be due to birds already being engaged in more stationary resting or scanning activities at higher temperatures and therefore not having to change behaviour to as large a degree to watch the approaching predator. In my analysis of the relationship between air temperature and bird activity (mobile vs stationary) across all temperatures, observations of stationary birds occurred at significantly higher temperatures than observations of mobile birds. Although the FIDs of mobile and stationary birds were not statistically significantly different, in the best-fit models (at high temperatures, low temperatures and across the full range of air temperatures) stationary birds tended to have shorter FIDs than mobile birds. This supports the suggestion that there may be reduced observational cost for stationary birds and they therefore wait longer before fleeing. The observational cost may also be *relatively* lower due to the increased thermoregulatory cost of fleeing at high temperatures. As discussed above, significantly shorter FIDs from cooler microsites (*Boscia albitrunca* and canopies in general) relative to warmer microsites at high air temperatures appear to give evidence of the significant effect of an increased thermoregulatory cost to fleeing at high temperatures.

The link between air temperature and microsite selection variables

My results show that air temperature had an effect on microsite selection for the birds in this study. Other studies have found similar results, e.g. Ricklefs and Hainsworth (1968) observed that increasing temperatures caused Cactus Wrens to forage in cooler microsites in the Lower Sonoran desert, Arizona; Austin and Miller (1982) found the same for migrant and resident birds in the northern Mojave Desert and Wolf *et al*. (1996) found that Black-tailed Gnatcatchers and a Verdin chose microsites that were significantly cooler when air temperatures were high in the Sonoran Desert. In my study, in both the cool temperature subset as well as data looking across the full range of air temperatures, birds were observed in the sun at significantly cooler air temperatures than when they were in the shade. Birds were also observed on tree tops at lower temperatures than when they were observed in the canopy (in the cool and full datasets) and on tree tops at lower temperatures than when they were on the ground (in the full dataset). By choosing cooler microsites when air temperatures are higher, birds are able to reduce their exposure to high environmental temperatures and can continue foraging for longer with reduced risk of reaching dangerous body temperature limits. Moving to cooler microsites also reduces the birds' need for evaporative cooling, which can have associated water-loss costs. This is particularly important for arid-zone birds where water availability is limiting. Wolf and Walsberg (1996) found that the rate of evaporative water loss for a Verdin sitting in a shaded microsite would be four times lower than if the bird was in the sun. Both bird exposure and location were found to explain some of the variation in FID, as discussed above. Air temperature is thus likely having an effect on FID via its influence on bird behaviour or microsite selection, even at cooler air temperatures where it may not be having a direct effect by imposing thermoregulatory constraints to fleeing.

Microsite temperature analysis

The operative temperature measured by black-bulb thermometers represents the combined effect of air temperature, solar radiation, conduction and convection in the microsite where they are placed (Bakken *et al*. 1985 in Cunningham *et al*. 2015). The measurement does not reflect the exact 'heat load' that birds in the microsite would experience as the effects of a bird's size, posture, colouration and plumage, as well as humidity and evaporation are not incorporated into the reading (Bakken *et al*. 1985 in Cunningham *et al*. 2015). The measurements are however useful for comparing the conditions (incorporating more than just air temperature) that birds would experience in different microsites (Cunningham *et al*. 2015).

Martin *et al*. (2015) measured the shade density of *Boscia albitrunca* and *Vachellia erioloba* trees in the Kalahari and found that *Boscia albitrunca* provided a greater level of shade than *Vachellia erioloba*. The black-bulb data from my study support this finding: mean black-bulb temperature in the shade of *Boscia albitrunca* trees was significantly lower than in the shade of *Vachellia erioloba.* My data also show that mean black-bulb temperature in the shade of *Senegalia mellifera* was significantly higher than the other two plant species. The shorter FIDs of birds from *Senegalia mellifera* bushes (significantly shorter than from *Vachellia erioloba* in the cool, hot and overall temperature datasets, and shorter than from *Boscia albitrunca* in all temperature datasets, but not significantly so) are thus not due to this plant offering a cooler microsite with higher thermal benefits, but likely due to the protection offered by this plant species, as discussed above.

Black-bulb temperature in the shade of *Boscia albitrunca* also increased more slowly with air temperature than in the shade of the other two plants. This means that the shade of *Boscia albitrunca* trees becomes increasingly the coolest place for birds to be as air temperatures rise. Martin *et al*. (2015) found that on hot days birds showed an increased preference for *Boscia albitrunca*. They point out the likely importance of these trees as a thermal refuge for birds in light of climate change and rising temperatures in the Kalahari.

Black-bulb temperature on the ground was higher, and increased faster with air temperature, than in the microsites above the ground, in both the shade and sun comparisons. Differences in mean black-bulb temperature between plant species were however not the same in the shade and sun comparisons. While mean black-bulb temperature in the shade was lowest in *Boscia albitrunca*, in the sun mean black-bulb temperature on *Vachellia erioloba* was significantly lower than on both *Boscia albitrunca* and *Senegalia mellifera*. The lower black-bulb temperature on *Vachellia erioloba* may be due to the canopy of this species being less dense (fewer branches and / or leaves) than the other two species, resulting in greater exposure to wind on *Vachellia erioloba*. Cunningham *et al*. (2015) found that the foraging success rates of Southern Fiscals *Lanius collaris* in the Kalahari were highest when they hunted from perches in the sun but that these birds switched to forage from perches in the shade at high air temperatures, likely due to a trade-off between foraging behaviour and thermoregulation. The reduced foraging success from the shade at high air temperatures may have fitness consequences for these birds (Cunningham *et al*. 2015). Trees such as *Vachellia erioloba* that provide thermal benefits (by providing cooler conditions) for birds, such as the Southern Fiscal, that benefit from perching in sunny locations but are limited by thermoregulatory constraints may become increasingly important in the landscape in light of the rising air temperatures associated with climate change.

Implications and further research

The indications in my data are that high air temperatures have an effect on reducing FID for the eight focal bird species in my study. With rising air temperatures in the Kalahari region due to climate change (Kruger and Sekele 2013; Cunningham *et al*. 2013a) this may have survival consequences for these species. If the birds are more frequently faced with the thermoregulatory challenges of fleeing at high temperatures, the resulting decrease in FID may lead to higher rates of predation on these species, and ultimately effects on population persistence. Alternatively, to avoid an increase in predation may result in birds more regularly being faced with rising body temperatures due to fleeing from cool microsites (e.g. a shady tree) at high air temperatures, with the consequent increased requirement for evaporative cooling and thus potential for dehydration (Wolf and Walsberg 1996). This too may have negative fitness or population persistence consequences for species (McKechnie and Wolf 2010). My data also indicate that there are differences in species with regard to FID. Unfortunately I did not have enough data at high temperatures to assess species individually at temperatures above 35 ^{o}C. I thus recommend that future studies on this topic should focus on collecting data at the higher end of the temperature range to determine whether certain species will be more affected by rising temperatures than others. This would help to identify species particularly vulnerable in the face of climate change. The other side of the predator-prey relationship would also need to be investigated (i.e. the effect of rising temperatures on the predators and how it affects their predation behaviour) to get a better understanding of the full picture of the effect of rising temperatures on predation in the Kalahari.

Conclusion

My study found that there is a negative relationship between air temperature and FID. This relationship is weak when looking across the full range of temperatures, with a large amount of variability in FID not explained by air temperature. However, air temperatures above 35 ^{o}C seem to be important in explaining some of the variation in FID. This is likely influenced by the thermoregulatory challenges facing birds when fleeing at high temperatures. Starting distance, bird species and the microsite selection variables (plant species, bird location and bird exposure) were consistently selected across all temperatures to explain some of the variation in FID. I suggest that the level of visibility of an approaching predator, the degree of shelter or protection offered by the different microsites and the thermal benefits of a particular microsite help explain the influence of microsite selection on FID in my data. The detectability of an approaching predator and the shelter or protection offered by a microsite appear to be important factors affecting FID across all temperatures and the thermal benefit (i.e. cooler operative temperature) of a microsite seems to be important when air temperatures are high. The influence of air temperature on some of the microsite selection choices of the birds reveals a potential mechanism through which air temperature may also indirectly be affecting FID. The reduction in FID at high air temperatures and thus the potentially increased risk of predation may have negative consequences for the bird species in my study, in light of rising air temperatures associated with climate change.

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Appendices

Appendix A

Table A1: Comparison of methods used in different studies to measure flight initiation distance (FID)

Study	**Species**	**Place**	**Method based on:**	**Starting distance**	**Pace of approach**	**FID = horizontal or Euclidian distance?**	**Notes**
Blumstein 2003	68 species	Australia and Tasmania	-	= focus of study; used a broad range; found significant positive linear relationship between starting distance and FID	0.5 ms^{-1}	Assume horizontal as don’t mention measuring height	Relationship between starting distance and FID varied by species
Blumstein *et al*. 2003	8 shorebirds	Australia	-	Doesn’t specify, other than to say the authors walked back to the starting location	0.5-1.0 ms^{-1}	Doesn’t specify, assume horizontal as spp are shorebirds	
Blumstein 2006	150 species	Australia, Europe and North America	Blumstein 2003	Recorded; starting distance found to explain significant variation in results	Steady pace of ~0.5 ms^{-1}	$FID_{direct} = \sqrt{FID_{horizontal}{}^2 + perching\ height^2}$	
Møller 2008	Multiple	France and Denmark	Blumstein 2006	Not mentioned	Normal walking speed	Euclidian distance	

Møller 2009	76 species	France and Denmark	“standardized technique” (as per Møller 2008)	Almost all individuals were approached from a distance of at least 30 m (no results changed statistically when including starting distance as an additional variable)	Normal walking speed	Euclidian distance	Euclidian distance used as large proportion of individuals were more than 5 m above ground level
Carrete and Tella 2010	Burrowing Owl (*Athene cunicularia*)	Argentina	-	Approximately 200 m	Constant speed of $0.5ms^{-1}$	Assume they used horizontal, as owls were usually ground-resting	
Weston *et al*. 2012	250 species	Australia	Used data from multiple studies, using various protocols; suggest Blumstein (2003) method has received “broadest patronage”				
Møller *et al*. 2014	193 species	Australia, Europe and North America	Used data from Blumstein 2006, Møller 2008 and Weston *et al*. 2012.				
Møller *et al*. 2015	61 species	France and Denmark	Blumstein 2006	Standardised to about 30m	Normal walking speed	Euclidian distance	

Appendix B

Table B1: The range of air temperatures (^{o}C) at which flight initiation distance (FID) measurements were taken for eight focal bird species in the Kalahari Desert in October and November 2015 and the number (and percentage) of the FID measurements taken at air temperatures of 35 ^{o}C and higher.

Bird species	**n**	**Minimum Ta (°C)**	**Maximum Ta (°C)**	**FIDs measured at Ta ≥ 35°C**	
				Number	**%**
Black-chested Prinia	91	12.7	38.9	14	15.4
Cape Turtle Dove	78	12.3	38.2	22	28.2
Chestnut-vented Tit-Babbler	83	12.4	38.2	13	15.7
Fawn-coloured Lark	71	12.1	38.4	19	26.8
Kalahari Scrub-Robin	65	12.7	40.3	16	24.6
Scaly-feathered Finch	137	12.3	40.4	33	24.1
Sociable Weaver	52	12.6	40.1	12	23.1
Yellow-bellied Eremomela	56	11.9	39.8	8	14.3
Total	633	11.9	40.4	137	21.6

Appendix C – Exploring indirect effects of air temperature on FID via effects on behaviour in three Kalahari bird species

Scaly-feathered Finch

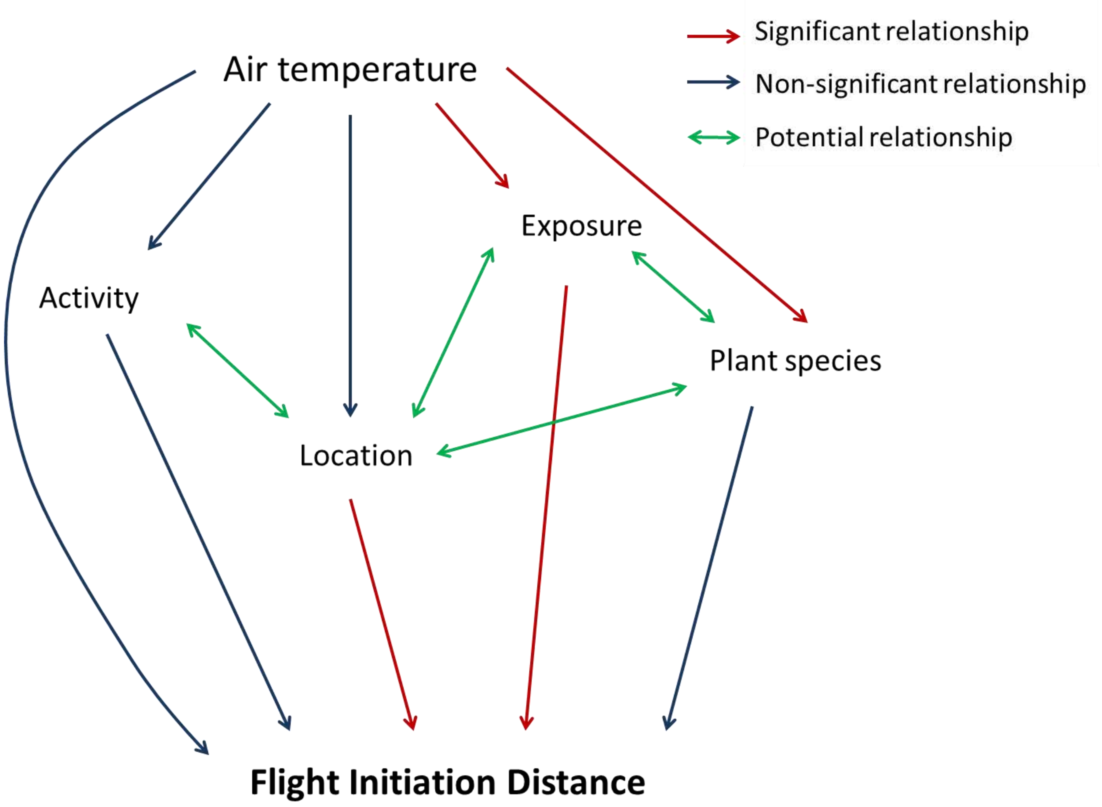

Figure C1: For Scaly-feathered Finches, air temperature did not have a significant effect on FID, although it may have an indirect effect via its influence on exposure (whether birds were in the shade or the sun). Both exposure and the location of the bird (canopy vs ground or tree top) affected FID.

There was no significant effect of air temperature on FID for Scaly-feathered Finches ($t = -1.09$; $n = 137$). Scaly-feathered Finches used *Senegalia mellifera* ($n = 56$) at significantly lower (4.2 ^{o}C, 95% CI: 0.9 – 7.5 ^{o}C) mean air temperature than *Vachellia erioloba* ($n = 43$), but FID was not significantly different between plant species for this bird (Figure C2 and Tables C1 and C2).

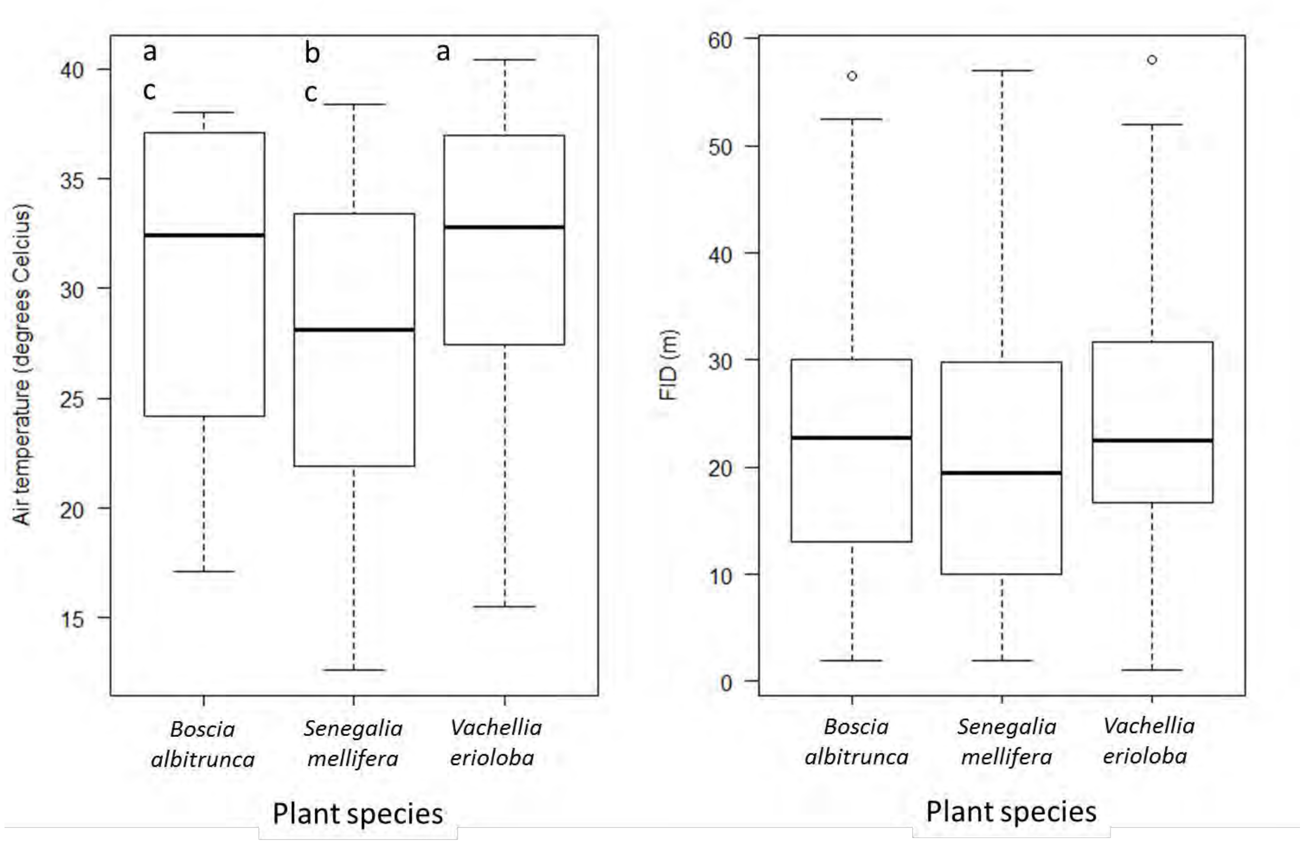

Figure C2: The air temperatures at which Scaly-feathered Finches used different plant species in this study (left). The FIDs for Scaly-feathered Finches when flushed from different plant species (right; *Boscia albitrunca* n = 18, *Senegalia mellifera* n = 56, *Vachellia erioloba* n = 43).

Table C1: Multiple comparisons of means (Tukey contrasts) of the air temperature (^{o}C) at which Scaly-feathered Finches used different plant species in the Kalahari Desert in October and November 2015.

Plant species comparisons	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**	**Significance code**
Senegalia mellifera - Boscia albitrunca	-3.34	1.89	-1.772	0.17602	
Vachellia erioloba - Boscia albitrunca	0.89	1.96	0.452	0.89222	
Vachellia erioloba - Senegalia mellifera	4.23	1.42	2.977	0.00792	**

Significance codes: *** < 0.001; ** < 0.01; * < 0.05; . < 0.1

Table C2: Multiple comparisons of means (Tukey contrasts) of the FID (m) of Scaly-feathered Finches when flushed from different plant species in the Kalahari Desert in October and November 2015.

Plant species comparisons	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**
Senegalia mellifera - Boscia albitrunca	-0.81	3.35	-0.242	0.968
Vachellia erioloba - Boscia albitrunca	3.49	3.46	1.008	0.568
Vachellia erioloba - Senegalia mellifera	4.3	2.51	1.716	0.196

There was no significant difference in mean air temperature between the observations of Scaly-feathered Finch in different locations, but mean FID was significantly shorter for birds flushed from the canopy of a tree (n = 75) than from the ground by 14.3 m (95% CI: 8.9 – 19.7 m; n = 35) and significantly shorter from the canopy than the top of a tree by 9.8 m (95% CI: 3.6 – 15.9 m; n = 22; Figure C3 and Tables C3 and C4).

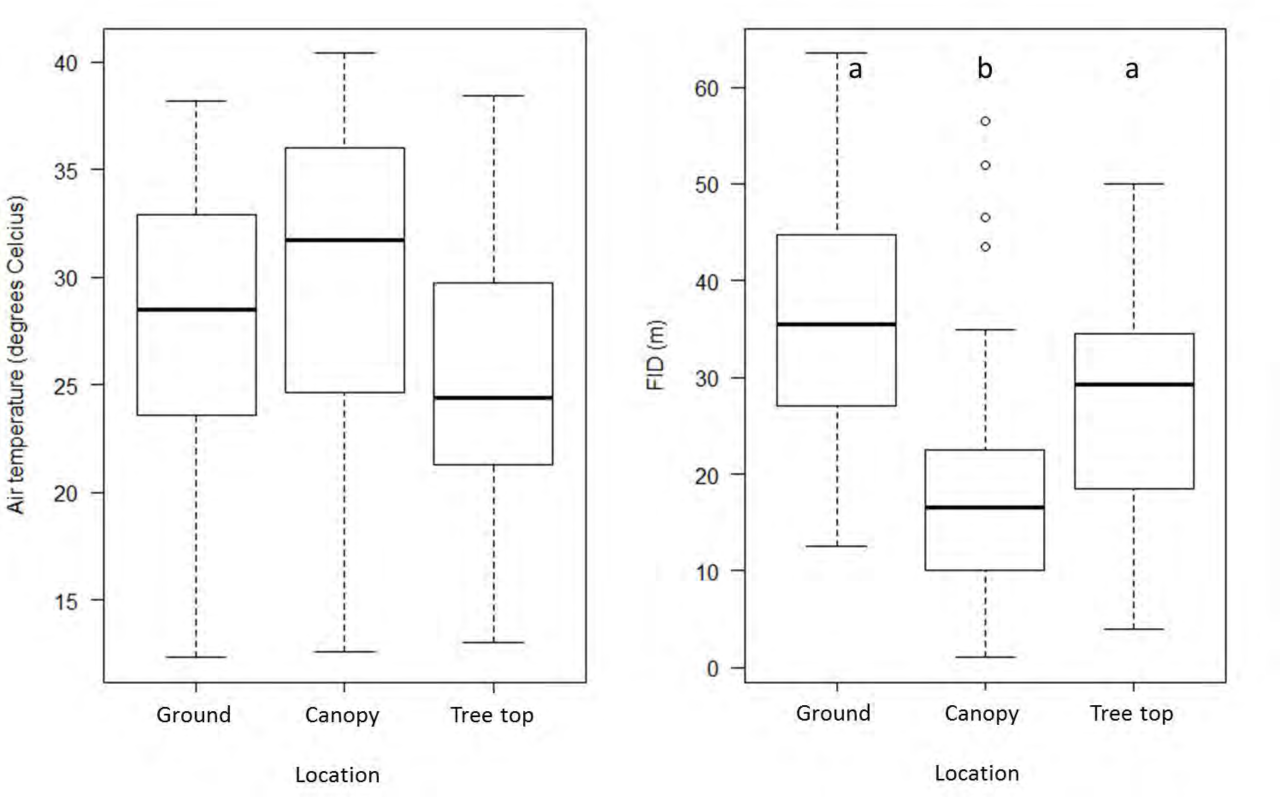

Figure C3: The air temperatures at which Scaly-feathered Finches used different locations in this study (left). FIDs of Scaly-feathered Finches when flushed from different locations (right; ground n = 35, canopy n = 75, tree top n = 22).

Table C3: Multiple comparisons of means (Tukey contrasts) of the air temperature (^{o}C) at which Scaly-feathered Finches used different locations in the Kalahari Desert in October and November 2015.

Location comparisons	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**
Ground - Canopy	-1.52	1.48	-1.027	0.556
Tree Top - Canopy	-3.51	1.76	-1.991	0.112
Tree Top - Ground	-1.99	1.97	-1.014	0.564

Table C4: Multiple comparisons of means (Tukey contrasts) of the FID (m) of Scaly-feathered Finches when flushed from different locations in the Kalahari Desert in October and November 2015.

Location comparisons	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**	**Significance code**
Ground - Canopy	14.32	2.32	6.184	<0.001	***
Tree Top - Canopy	9.75	2.63	3.715	<0.001	***
Tree Top - Ground	-4.57	3.07	-1.489	0.292	

Significance codes: *** < 0.001; ** < 0.01; * < 0.05; . < 0.1

Mean air temperature for Scaly-feathered Finches observed in the sun (n = 41) was significantly lower than for birds in the shade (a difference of 7.6 ^{o}C, 95% CI: 4.9 – 10.3 ^{o}C, t = - 5.71, n = 55) and mean FID was significantly longer for birds observed in the sun than for birds in the shade (a difference of 5.3 m, 95% CI: 0.7 – 9.9 m, t = 2.28; Figure C4).

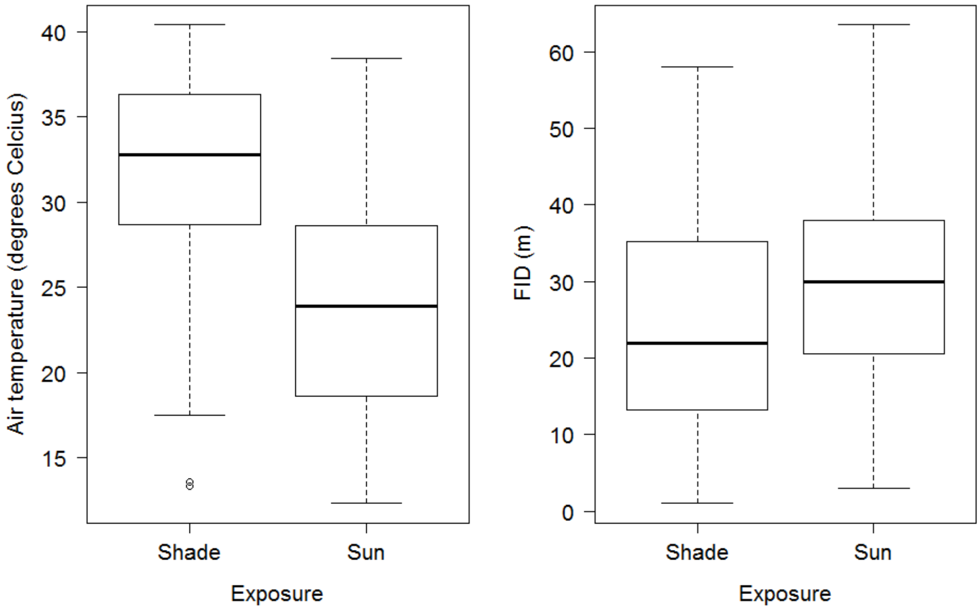

Figure C4: The air temperatures at which Scaly-feathered Finches were observed in the shade and in the sun in this study (left). FIDs of Scaly-feathered Finches flushed from the shade and from the sun (right; shade n = 55, sun n = 41).

There was no significant effect of air temperature on Scaly-feathered Finch activity (t = -0.72). FID tended to be longer in mobile (n = 29) than stationary (n = 67) birds, however this trend was not significant (t = -1.88; Figure C5).

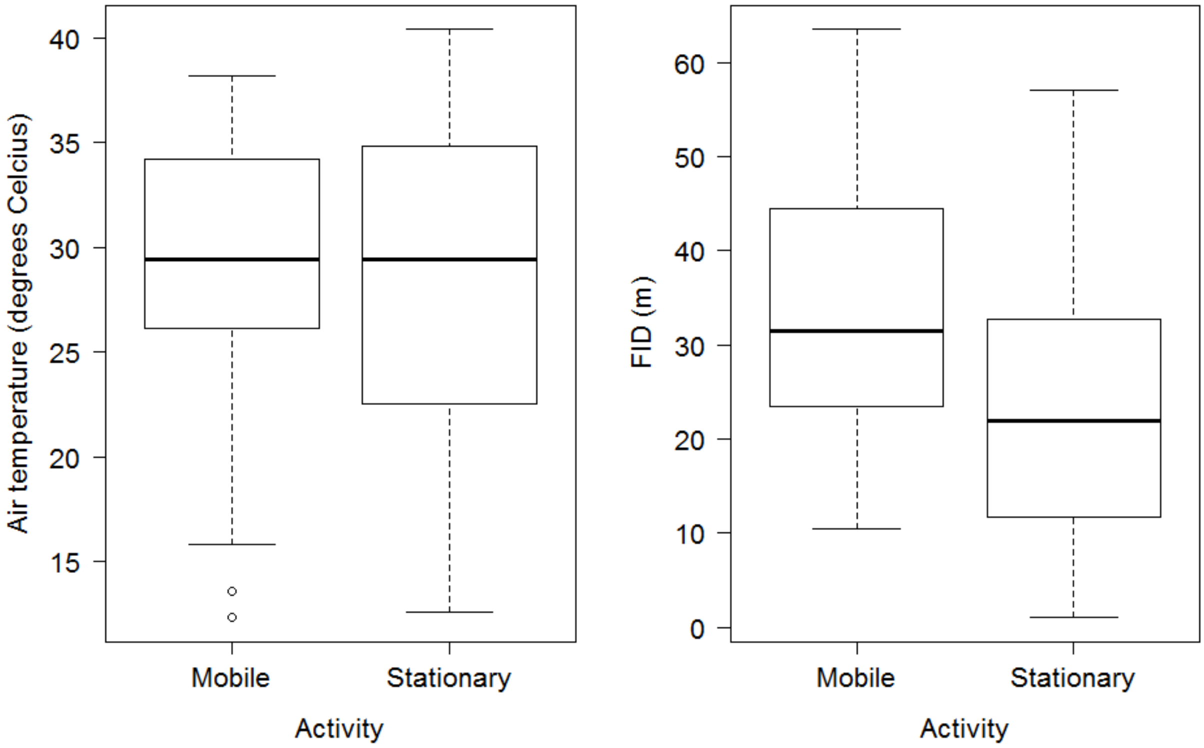

Figure C5: The air temperature at which mobile and stationary Scaly-feathered Finches were observed in this study (left). FIDs of mobile and stationary Scaly-feathered Finches (right; mobile = 29, stationary = 67).

Fawn-coloured Lark

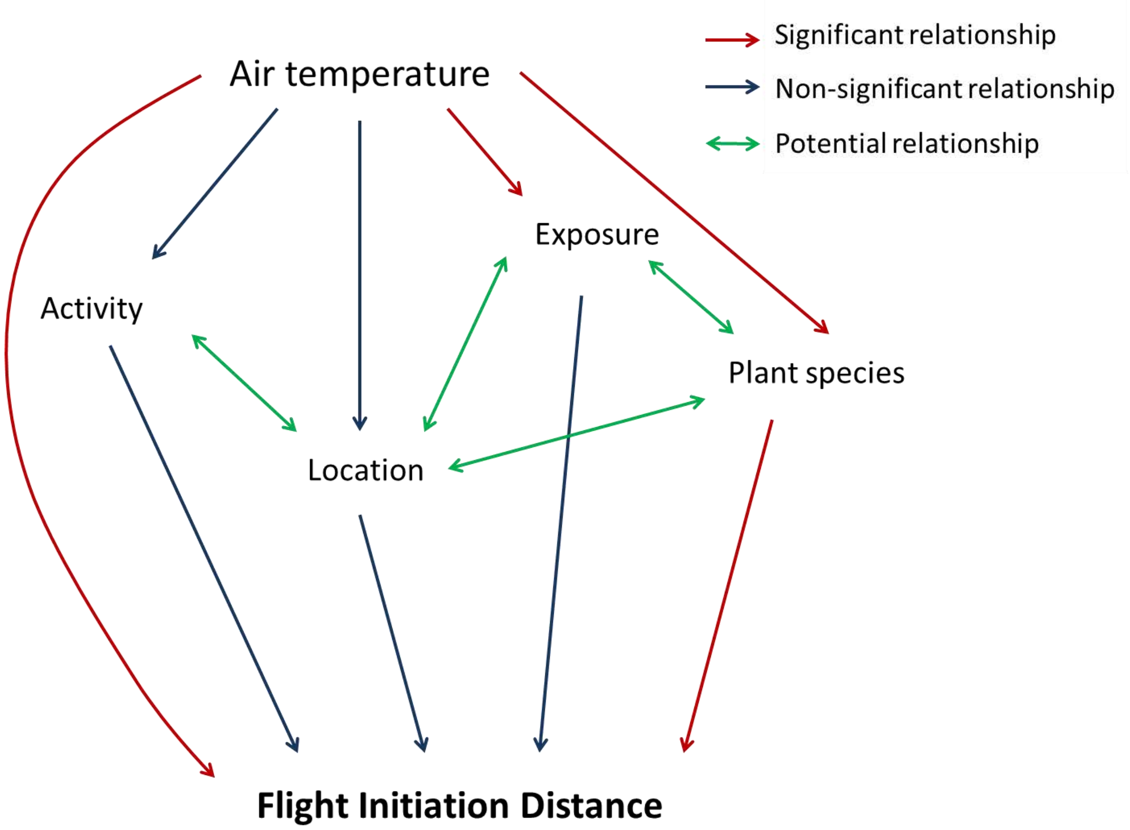

Figure C6: Air temperature was found to have a significant effect on FID for Fawn-coloured Larks. In addition, it may have an indirect effect via its influence on the plants Fawn-coloured Larks use, which were found to affect FID. While air temperature had an effect on exposure (whether birds were in the shade or the sun) this factor was not found to have an effect on FID for this species.

Air temperature had a significant negative effect on FID for Fawn-coloured Larks (t = -2.61; n = 71). There was an estimated 0.46 m decrease in FID for each 1 ^{o}C rise in air temperature (95% CI: -0.8 - -0.1 m).

Fawn-coloured larks were observed in/under *Senegalia mellifera* (n = 18) at significantly higher mean air temperature than when they were in/under dead trees (a difference of 6.5 ^{o}C, 95% CI: 1.8 – 11.2 ^{o}C; n = 8). Furthermore, the mean FID of Fawn-coloured Larks when flushed from *Senegalia mellifera* was significantly shorter than when flushed from dead trees by 9.8 m (95% CI: 0.7 – 18.8 m) or from *Vachellia erioloba* by 11.1 m (95% CI: 4.2 – 17.95 m; n = 21; Figure C7 and Tables C5 and C6).

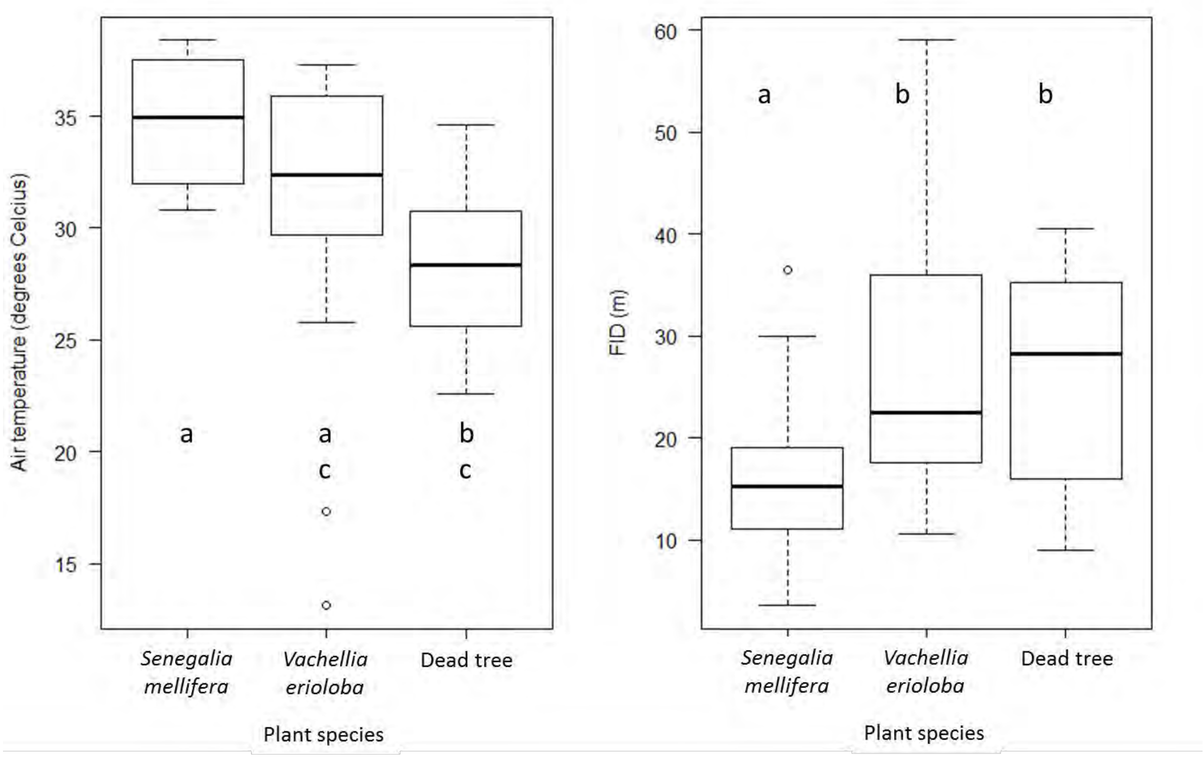

Figure C7: The air temperatures at which Fawn-coloured larks were observed in/under different plant species in this study (left). FIDs of Fawn-coloured Larks when flushed from different plant species (right; *Senegalia mellifera* n = 18, *Vachellia erioloba* n = 21, Dead tree n = 8).

Table C5: Multiple comparisons of means (Tukey contrasts) of the air temperature (^{o}C) at which Fawn-coloured Larks used different plant species in the Kalahari Desert in October and November 2015.

Plant species comparisons	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**	**Significance code**
Senegalia mellifera - Dead tree	6.49	2.03	3.205	0.00379	**
Vachellia erioloba - Dead tree	2.92	1.98	1.475	0.29957	
Vachellia erioloba - Senegalia mellifera	-3.57	1.53	-2.331	0.05075	.

Significance codes: *** < 0.001; ** < 0.01; * < 0.05; . < 0.1

Table C6: Multiple comparisons of means (Tukey contrasts) of the FID (m) of Fawn-coloured Larks when flushed from different plant species in the Kalahari Desert in October and November 2015.

Plant species comparisons	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**	**Significance code**
Senegalia mellifera - Dead tree	-9.76	3.88	-2.515	0.03134	*
Vachellia erioloba - Dead tree	1.31	3.80	0.345	0.935861	
Vachellia erioloba - Senegalia mellifera	11.07	2.95	3.757	0.000505	***

Significance codes: *** < 0.001; ** < 0.01; * < 0.05; . < 0.1

There was no significant difference in mean air temperature (t = -1.3) for observations of Fawn-coloured Larks on the ground (n = 50) compared to on the top of a tree (n = 13; there were insufficient data in the other location categories to include them in the model). There was also no significant difference in FID between Fawn-coloured Larks when flushed from these two locations (t = 0.96; Figure C8).

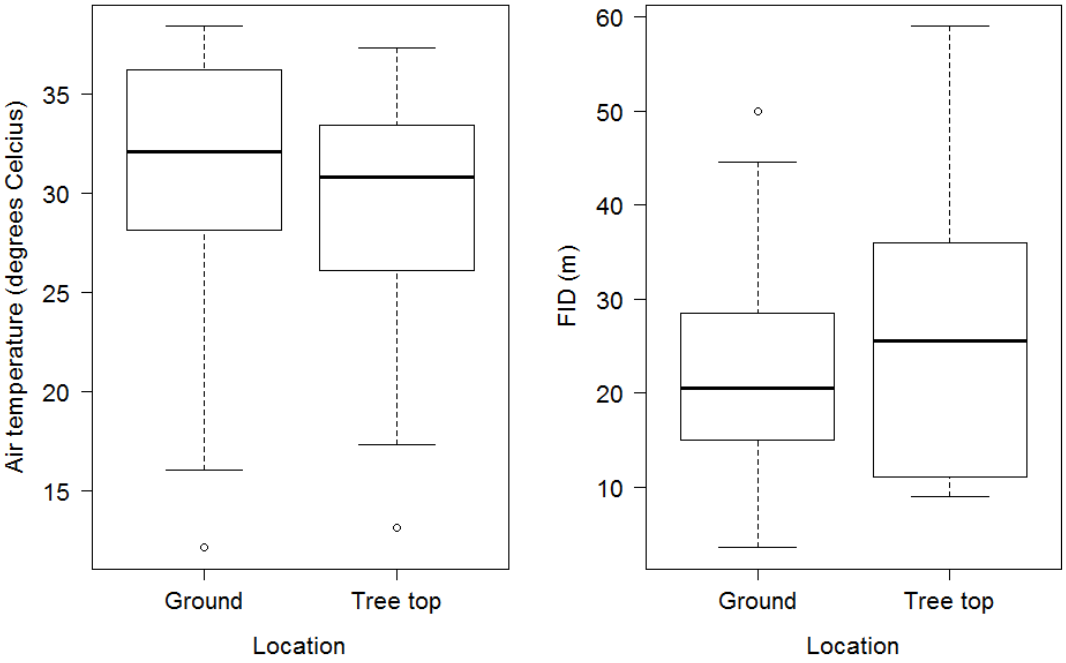

Figure C8: The air temperatures at which Fawn-coloured Larks were observed on the ground and on tree tops in this study (left). FIDs of Fawn-coloured Larks from the ground and from tree tops (right; ground n = 50, tree top n = 13).

Fawn-coloured Larks were observed in the sun (n = 24) at significantly cooler mean air temperatures than birds in the shade (a difference of 5.9 ^{o}C, 95% CI: 3.1 – 8.6 ^{o}C; t = - 4.19; n = 41; Figure C9). Mean FID was not significantly different between Fawn-coloured Larks in the shade and those in the sun (t = 1.74).

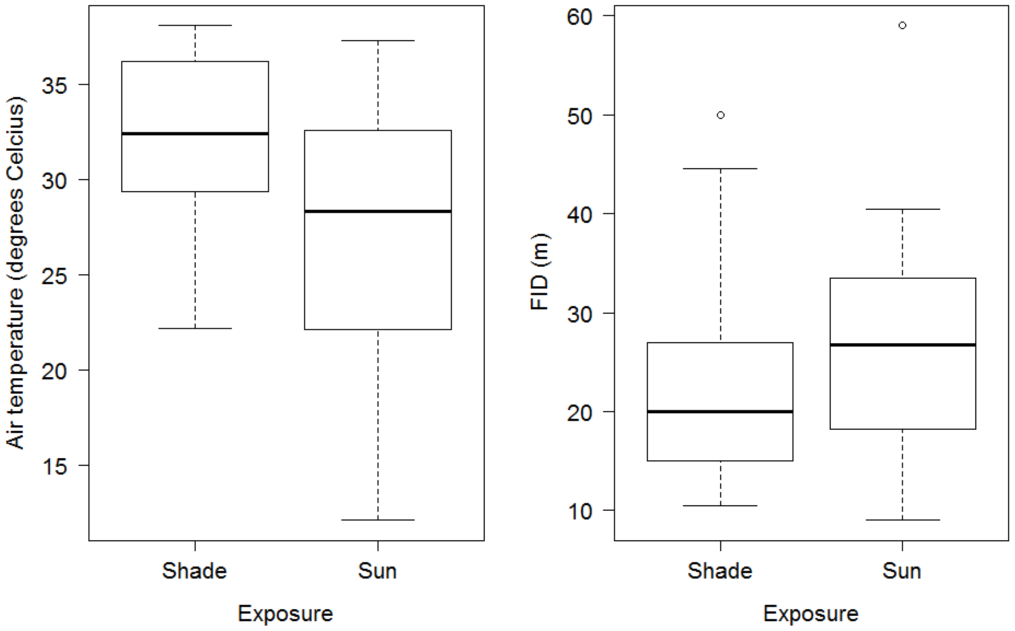

Figure C9: The air temperatures at which Fawn-coloured Larks were observed in the shade and in the sun in this study (left). FIDs of Fawn-coloured Larks when flushed from the shade and from the sun (right; shade n = 41, sun n = 24).

There was no significant difference in mean air temperature between observations of mobile (n = 26) and stationary (n = 39) Fawn-coloured Larks in this study (t = 1.27), nor was mean FID significantly different between mobile and stationary birds (t = -0.73; Figure C10).

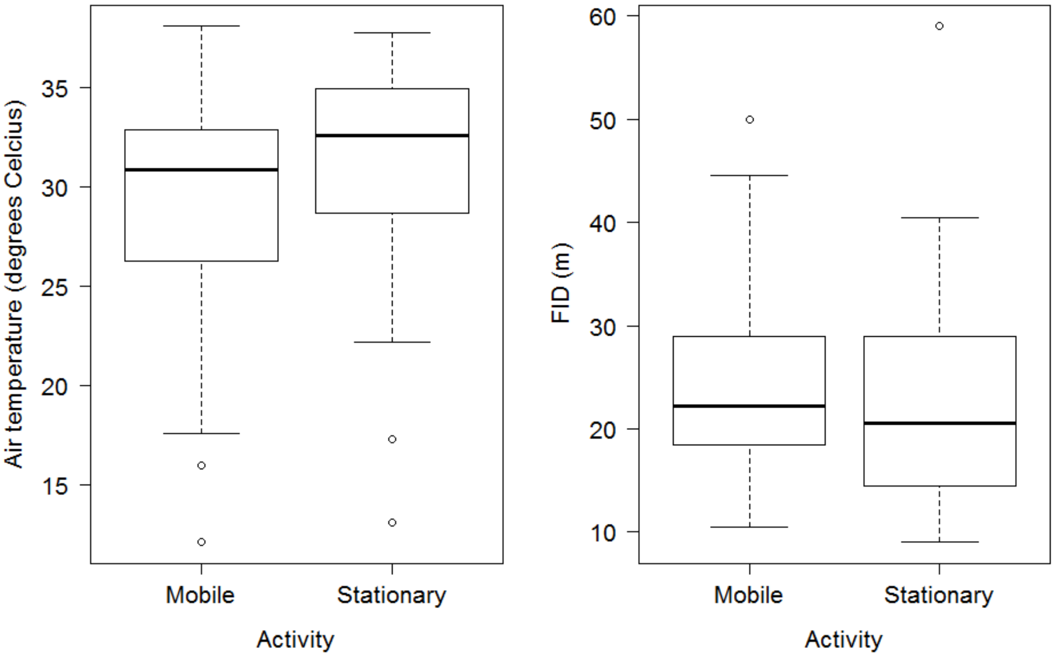

Figure C10: The air temperatures at which mobile and stationary Fawn-coloured Larks were observed in this study (left). FIDs of mobile and stationary Fawn-coloured Larks (right; mobile = 26, stationary = 39).

Cape Turtle Dove

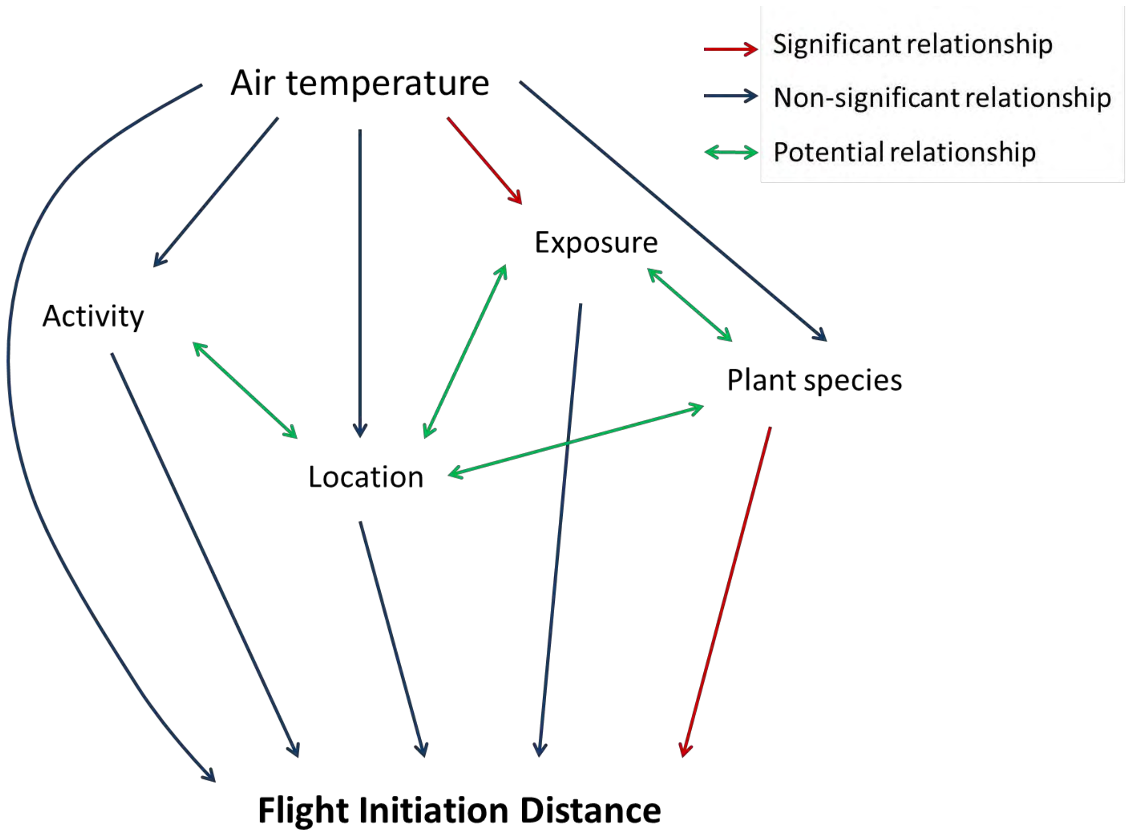

Figure C11: Air temperature did not have a significant effect on FID for Cape Turtle Doves. While air temperature had an effect on exposure (whether birds were in the shade or the sun) this factor was not found to have an effect on FID for this species. The plant species the Cape Turtle Doves were in (*Boscia albitrunca* or *Vachellia erioloba*) affected FID, but air temperature was not found to impact which of these two trees the Cape Turtle Doves were in.

There was no significant effect of air temperature on FID for Cape Turtle Doves (t = 0.27; n = 78).

There was no significant difference in mean air temperature between Cape Turtle Doves observed in *Boscia albitrunca* (n = 36) and those observed in *Vachellia erioloba* (t = 0.36; n = 24; Figure C12) (other plant species were excluded from the model due to insufficient observations of Cape Turtle Doves in those plants). Cape Turtle Doves in / under *Vachellia erioloba* had significantly longer FIDs than birds in / under *Boscia albitrunca* by an average of 10.2 m (95% CI: 2.6 – 17.8 m; t = 2.64; Figure C12).

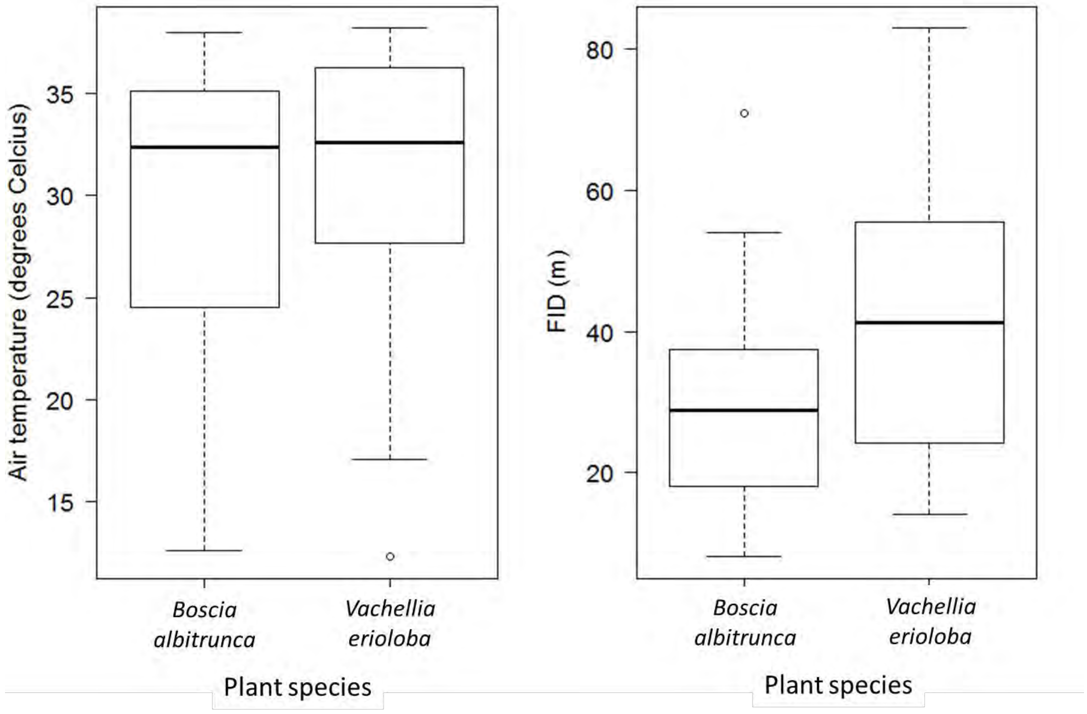

Figure C12: The air temperatures at which Cape Turtle Doves were observed using *Boscia albitrunca* and *Vachellia erioloba* plants in this study (left). FIDs of Cape Turtle Doves when flushed from in / under *Boscia albitrunca* and *Vachellia erioloba* plants (right; *Boscia albitrunca* n = 36, *Vachellia erioloba* n = 24).

There was no significant difference in mean air temperature between observations of Cape Turtle Doves on the ground (n = 49) and those in the canopy (t = -0.53; n = 24; Figure C13). FIDs from the canopy or from the ground were also not significantly different for this bird (t = 0.25; Figure C13).

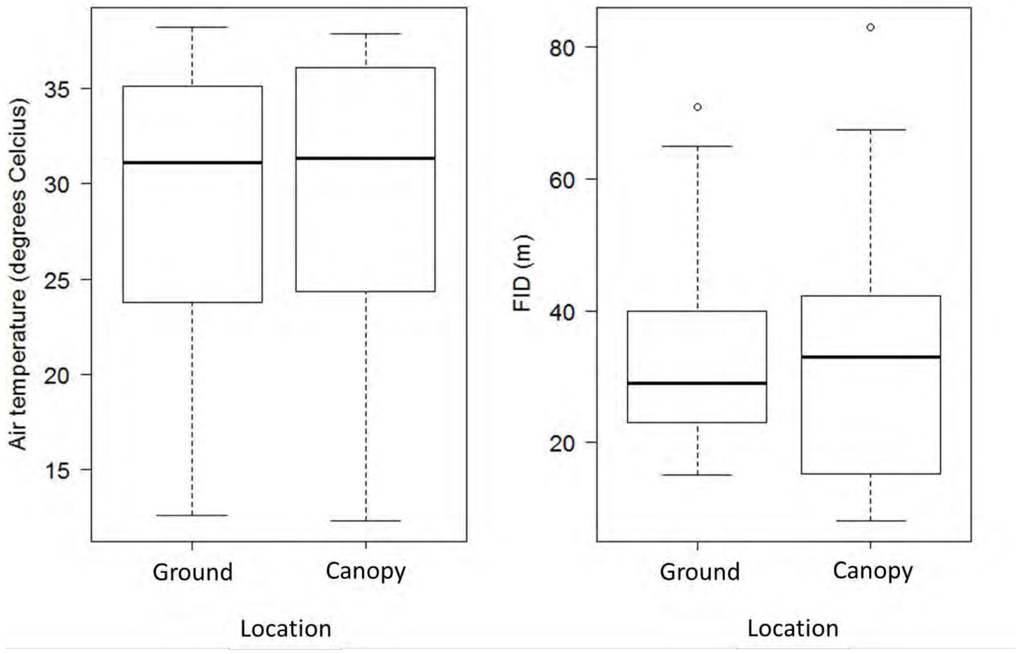

Figure C13: The air temperatures at which Cape Turtle Doves were observed on the ground or in the canopy of a tree in this study (left). FIDs of Cape Turtle Doves flushed from the ground or from the canopy of a tree (right; ground n = 49, canopy n = 24).

Cape Turtle Doves were observed in the sun (n = 11) at a significantly cooler mean air temperature than when observed in the shade (difference of 8.4 ^{o}C, 95% CI: 4.4 – 12.3 ^{o}C; t = -4.14; n = 47), however there was no significant difference in mean FID between Cape Turtle Doves in the sun and in the shade (t = 0.52; Figure C14).

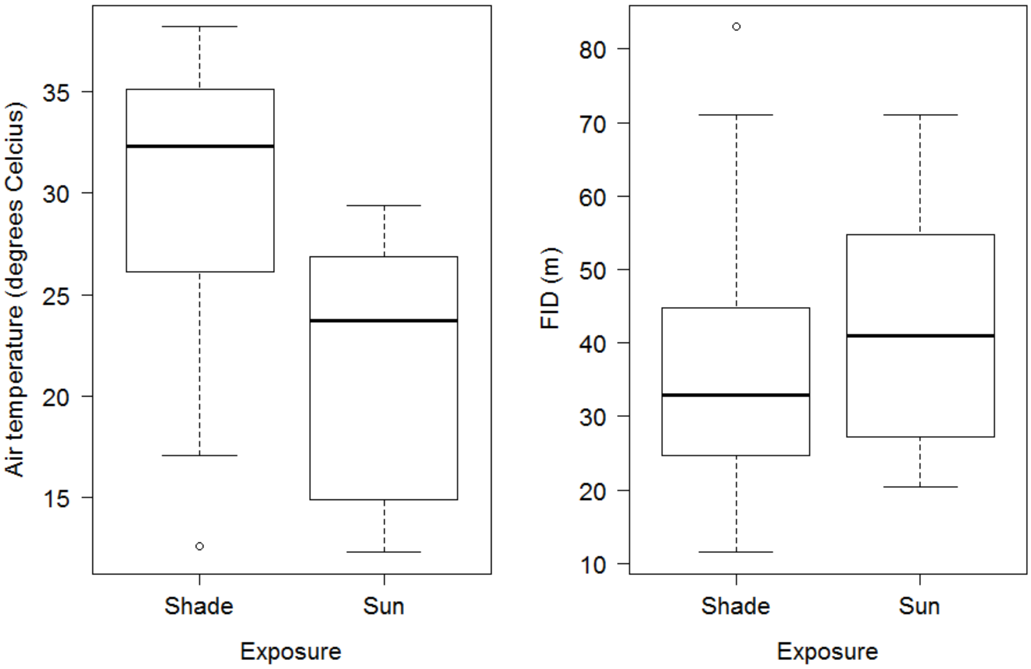

Figure C14: The air temperatures at which Cape Turtle Doves were observed in the shade and in the sun in this study (left). FIDs of Cape Turtle Doves when flushed from the shade and from the sun (right; shade n = 47, sun n = 11).

Mobile (n = 27) and stationary (n = 31) Cape Turtle Doves were not observed at significantly different mean air temperatures (t = -0.09) and were not found to have significantly different FIDs (t = 0.05; Figure C15).

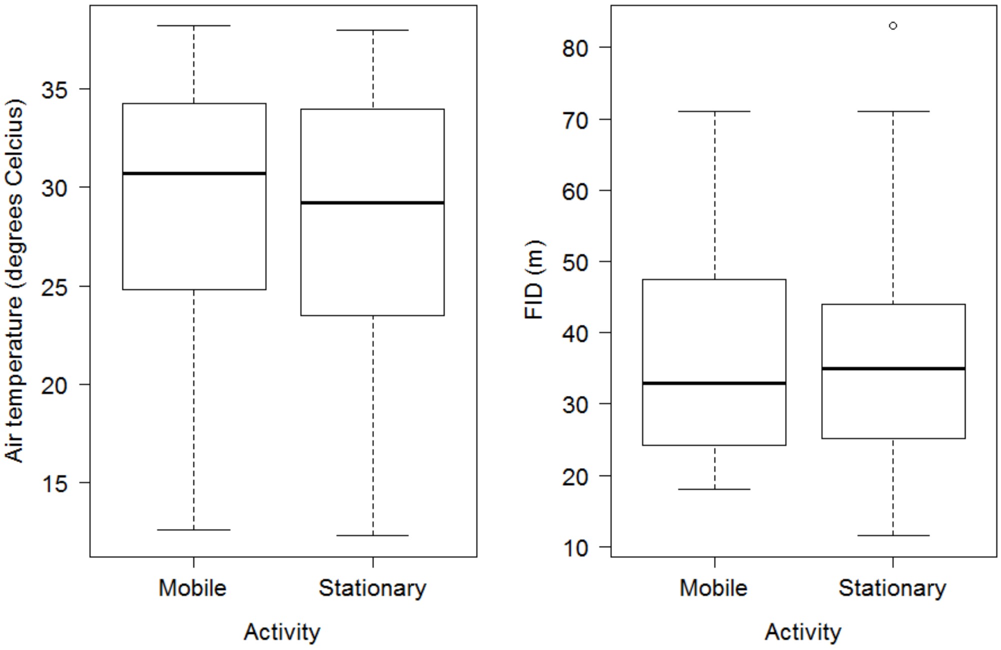

Figure C15: The air temperatures at which mobile and stationary Cape Turtle Doves were observed in this study (left). FIDs of mobile and stationary Cape Turtle Doves (right; mobile n = 27, stationary = 31).

Appendix D – Tukey comparisons

Single variable analyses

Table D1: Multiple comparisons of means (Tukey contrasts) of the FID (m) of eight focal bird species between plant species in the Kalahari Desert in October and November 2015. Model: FID ~ (transect) + starting distance + plant species.

Plant species comparisons	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**	**Significance code**
Dead tree - *Boscia albitrunca*	9.36	2.71	3.459	0.00416	**
Rhigozum trichotomum - Boscia albitrunca	7.95	2.98	2.665	0.05086	.
Senegalia mellifera - Boscia albitrunca	-0.60	1.40	-0.429	0.99194	
Vachellia erioloba - Boscia albitrunca	4.07	1.35	3.014	0.01849	*
Rhigozum trichotomum - Dead tree	-1.41	3.70	-0.38	0.99494	
Senegalia mellifera - Dead tree	-9.96	2.61	-3.814	0.0011	**
Vachellia erioloba - Dead tree	-5.29	2.59	-2.046	0.21957	
Senegalia mellifera - Rhigozum trichotomum	-8.55	2.87	-2.982	0.02053	*
Vachellia erioloba - Rhigozum trichotomum	-3.89	2.86	-1.358	0.62654	
Vachellia erioloba - Senegalia mellifera	4.67	1.11	4.208	< 0.001	***

Significance codes: *** < 0.001; ** < 0.01; * < 0.05; . < 0.1

Table D2: Multiple comparisons of means (Tukey contrasts) of the air temperature (^{o}C) at which eight focal bird species used different plants in the Kalahari Desert in October and November 2015. Model: Air temperature ~ (transect) + plant species.

Plant species comparisons	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**	**Significance code**
Dead tree - *Boscia albitrunca*	-2.39	1.58	-1.517	0.5211	
Rhigozum trichotomum - Boscia albitrunca	-4.53	1.73	-2.616	0.0584	.
Senegalia mellifera - Boscia albitrunca	-1.06	0.80	-1.321	0.6513	
Vachellia erioloba - Boscia albitrunca	0.21	0.79	0.268	0.9987	
Rhigozum trichotomum - Dead tree	-2.15	2.14	-1.001	0.8394	
Senegalia mellifera - Dead tree	1.33	1.52	0.879	0.8937	
Vachellia erioloba - Dead tree	2.60	1.51	1.719	0.3918	
Senegalia mellifera - Rhigozum trichotomum	3.48	1.68	2.07	0.2097	
Vachellia erioloba - Rhigozum trichotomum	4.75	1.68	2.828	0.0323	*
Vachellia erioloba - Senegalia mellifera	1.27	0.65	1.967	0.2564	

Significance codes: *** < 0.001; ** < 0.01; * < 0.05; . < 0.1

Table D3: Multiple comparisons of means (Tukey contrasts) of the FID (m) between birds in different locations in the Kalahari Desert in October and November 2015. Model: FID ~ (transect) + starting distance + bird location.

Bird location comparisons	Estimate	Std. Error	z value	Pr(>|z|)	Significance code
Dead Tree - Canopy	11.48	2.90	3.952	<0.001	***
Ground - Canopy	7.14	1.05	6.806	<0.001	***
Tree Top - Canopy	6.71	1.37	4.882	<0.001	***
Ground - Dead Tree	-4.33	2.96	-1.464	0.434	
Tree Top - Dead Tree	-4.77	3.10	-1.54	0.388	
Tree Top - Ground	-0.44	1.51	-0.289	0.991	

Significance codes: *** < 0.001; ** < 0.01; * < 0.05; . < 0.1

Table D4: Multiple comparisons of means (Tukey contrasts) of the air temperature (^{o}C) at which eight focal bird species used different locations in the Kalahari Desert in October and November 2015. Model: Air temperature ~ (transect) + bird location.

Bird location comparisons	Estimate	Std. Error	z value	Pr(>|z|)	Significance code
Dead Tree - Canopy	-0.70	1.75	-0.399	0.976	
Ground - Canopy	-0.25	0.62	-0.406	0.975	
Tree Top - Canopy	-3.63	0.84	-4.332	<0.001	***
Ground - Dead Tree	0.45	1.79	0.252	0.994	
Tree Top - Dead Tree	-2.93	1.87	-1.569	0.371	
Tree Top - Ground	-3.38	0.90	-3.75	<0.001	***

Significance codes: *** < 0.001; ** < 0.01; * < 0.05; . < 0.1

Full model analyses - Tukey comparisons of mean FID at different levels of factors included in top models of FID across eight Kalahari bird species

Across all air temperatures

Table D5: Multiple comparisons of means (Tukey contrasts) of the FID (m) of eight focal bird species between different times of day in the Kalahari Desert in October and November 2015, from Model 1, Table 1: FID ~ (transect) + starting distance + time of day + bird species + plant species + location + exposure + activity.

Time of day comparisons	Estimate	Std. Error	z value	Pr(>|z|)
Early morning - Afternoon	0.95	1.24	0.764	0.724
Late morning - Afternoon	0.92	1.09	0.845	0.675
Late morning - Early morning	-0.03	1.25	-0.024	1

Table D6: Multiple comparisons of means (Tukey contrasts) of FID (m) between eight focal bird species in the Kalahari Desert in October and November 2015, from Model 1, Table 1: FID ~ (transect) + starting distance + time of day + bird species + plant species + location + exposure + activity.

Bird species comparisons	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**	**Significance code**
Cape Turtle Dove - Black-chested Prinia	9.30	2.42	3.84	0.00297	**
Chestnut-vented Tit-Babbler - Black-chested Prinia	-1.29	1.89	-0.683	0.99718	
Fawn-coloured Lark - Black-chested Prinia	3.48	2.46	1.413	0.84228	
Kalahari Scrub-Robin - Black-chested Prinia	5.90	2.25	2.618	0.1419	
Scaly-feathered Finch - Black-chested Prinia	4.75	2.02	2.355	0.25251	
Sociable Weaver - Black-chested Prinia	5.57	2.38	2.343	0.25846	
Yellow-bellied Eremomela - Black-chested Prinia	1.99	1.97	1.011	0.97052	
Chestnut-vented Tit-Babbler - Cape Turtle Dove	-10.60	2.39	-4.431	< 0.001	***
Fawn-coloured Lark - Cape Turtle Dove	-5.83	2.00	-2.916	0.06547	.
Kalahari Scrub-Robin - Cape Turtle Dove	-3.40	2.11	-1.612	0.73033	
Scaly-feathered Finch - Cape Turtle Dove	-4.55	1.78	-2.556	0.16415	
Sociable Weaver - Cape Turtle Dove	-3.74	2.10	-1.778	0.6205	
Yellow-bellied Eremomela - Cape Turtle Dove	-7.31	2.52	-2.902	0.06828	.
Fawn-coloured Lark - Chestnut-vented Tit-Babbler	4.77	2.53	1.885	0.54657	
Kalahari Scrub-Robin - Chestnut-vented Tit-Babbler	7.19	2.31	3.11	0.03771	*
Scaly-feathered Finch - Chestnut-vented Tit-Babbler	6.04	2.09	2.888	0.07075	.
Sociable Weaver - Chestnut-vented Tit-Babbler	6.86	2.40	2.857	0.07776	.
Yellow-bellied Eremomela - Chestnut-vented Tit-Babbler	3.28	1.96	1.673	0.69149	
Kalahari Scrub-Robin - Fawn-coloured Lark	2.42	2.06	1.174	0.93473	
Scaly-feathered Finch - Fawn-coloured Lark	1.27	1.80	0.709	0.99643	
Sociable Weaver - Fawn-coloured Lark	2.09	2.14	0.977	0.97575	
Yellow-bellied Eremomela - Fawn-coloured Lark	-1.49	2.62	-0.569	0.99913	
Scaly-feathered Finch - Kalahari Scrub-Robin	-1.15	1.83	-0.628	0.99834	
Sociable Weaver - Kalahari Scrub-Robin	-0.33	2.19	-0.151	1	
Yellow-bellied Eremomela - Kalahari Scrub-Robin	-3.91	2.41	-1.624	0.72301	
Sociable Weaver - Scaly-feathered Finch	0.82	1.85	0.441	0.99984	
Yellow-bellied Eremomela - Scaly-feathered Finch	-2.76	2.20	-1.255	0.90922	
Yellow-bellied Eremomela - Sociable Weaver	-3.58	2.47	-1.448	0.82512	

Significance codes: *** < 0.001; ** < 0.01; * < 0.05; . < 0.1

Table D7: Multiple comparisons of means (Tukey contrasts) of the FID (m) of eight focal bird species flushed from different plants in the Kalahari Desert in October and November 2015, from Model 1, Table 1: FID ~ (transect) + starting distance + time of day + bird species + plant species + location + exposure + activity.

Plant species comparisons	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**	**Significance code**
Boscia albitrunca - Open ground	0.65	2.25	0.287	0.9997	
Dead tree - Open ground	-1.01	4.72	-0.214	0.9999	
Rhigozum trichotomum - Open ground	4.71	3.26	1.448	0.6632	
Senegalia mellifera - Open ground	-2.72	2.05	-1.331	0.7379	
Vachellia erioloba - Open ground	1.95	2.08	0.936	0.9262	
Dead tree - *Boscia albitrunca*	-1.65	4.57	-0.362	0.999	
Rhigozum trichotomum - *Boscia albitrunca*	4.07	3.02	1.348	0.7272	
Senegalia mellifera - *Boscia albitrunca*	-3.37	1.67	-2.02	0.2951	
Vachellia erioloba - *Boscia albitrunca*	1.30	1.60	0.814	0.9584	
Rhigozum trichotomum - Dead tree	5.72	4.92	1.163	0.833	
Senegalia mellifera - Dead tree	-1.71	4.38	-0.392	0.9985	
Vachellia erioloba - Dead tree	2.95	4.39	0.673	0.9818	
Senegalia mellifera - *Rhigozum trichotomum*	-7.44	2.71	-2.747	0.0554	.
Vachellia erioloba - *Rhigozum trichotomum*	-2.77	2.77	-0.998	0.9051	
Vachellia erioloba - *Senegalia mellifera*	4.67	1.14	4.082	<0.001	***

Significance codes: *** < 0.001; ** < 0.01; * < 0.05; . < 0.1

Table D8: Multiple comparisons of means (Tukey contrasts) of the FID (m) of eight focal bird species flushed from different locations in the Kalahari Desert in October and November 2015, from Model 1, Table 1: FID ~ (transect) + starting distance + time of day + bird species + plant species + location + exposure + activity.

Bird location comparisons	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**
Dead Tree - Canopy	10.30	5.31	1.938	0.187
Ground - Canopy	3.07	1.72	1.789	0.25
Tree Top - Canopy	2.66	1.80	1.477	0.418
Ground - Dead Tree	-7.23	5.57	-1.297	0.532
Tree Top - Dead Tree	-7.64	5.09	-1.5	0.404
Tree Top - Ground	-0.41	2.29	-0.18	0.998

At air temperatures of 35 ^{o}C and higher

Table D9: Multiple comparisons of means (Tukey contrasts) of FID (m) between eight focal bird species at air temperatures of 35 ^{o}C and above in the Kalahari Desert in October and November 2015, from the model in Table 3: FID ~ (transect) + air temperature + starting distance + time of day + bird species + plant species + location + activity.

Bird species comparisons	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**	**Significance code**
Cape Turtle Dove - Black-chested Prinia	11.50	5.07	2.266	0.2963	
Chestnut-vented Tit-Babbler - Black-chested Prinia	3.83	4.04	0.948	0.979	
Fawn-coloured Lark - Black-chested Prinia	3.59	5.36	0.67	0.9974	
Kalahari Scrub-Robin - Black-chested Prinia	16.89	4.43	3.81	0.0033	**
Scaly-feathered Finch - Black-chested Prinia	8.18	4.03	2.029	0.4428	
Sociable Weaver - Black-chested Prinia	1.02	5.04	0.203	1	
Yellow-bellied Eremomela - Black-chested Prinia	3.01	4.94	0.61	0.9986	
Chestnut-vented Tit-Babbler - Cape Turtle Dove	-7.67	4.67	-1.642	0.7078	
Fawn-coloured Lark - Cape Turtle Dove	-7.90	3.81	-2.071	0.4155	
Kalahari Scrub-Robin - Cape Turtle Dove	5.40	4.45	1.213	0.9214	
Scaly-feathered Finch - Cape Turtle Dove	-3.31	3.53	-0.938	0.9803	
Sociable Weaver - Cape Turtle Dove	-10.47	4.29	-2.442	0.2087	
Yellow-bellied Eremomela - Cape Turtle Dove	-8.48	5.69	-1.491	0.7987	
Fawn-coloured Lark - Chestnut-vented Tit-Babbler	-0.24	5.10	-0.046	1	
Kalahari Scrub-Robin - Chestnut-vented Tit-Babbler	13.06	4.35	3.005	0.0501	.
Scaly-feathered Finch - Chestnut-vented Tit-Babbler	4.35	3.78	1.153	0.9392	
Sociable Weaver - Chestnut-vented Tit-Babbler	-2.80	4.72	-0.595	0.9988	
Yellow-bellied Eremomela - Chestnut-vented Tit-Babbler	-0.82	4.64	-0.176	1	
Kalahari Scrub-Robin - Fawn-coloured Lark	13.30	4.70	2.828	0.0823	.
Scaly-feathered Finch - Fawn-coloured Lark	4.59	3.84	1.197	0.9266	
Sociable Weaver - Fawn-coloured Lark	-2.57	4.72	-0.544	0.9993	
Yellow-bellied Eremomela - Fawn-coloured Lark	-0.58	6.21	-0.094	1	
Scaly-feathered Finch - Kalahari Scrub-Robin	-8.71	3.72	-2.339	0.2582	
Sociable Weaver - Kalahari Scrub-Robin	-15.87	4.89	-3.244	0.0244	*
Yellow-bellied Eremomela - Kalahari Scrub-Robin	-13.88	5.31	-2.612	0.1423	
Sociable Weaver - Scaly-feathered Finch	-7.16	4.08	-1.755	0.6325	
Yellow-bellied Eremomela - Scaly-feathered Finch	-5.17	4.98	-1.04	0.9649	
Yellow-bellied Eremomela - Sociable Weaver	1.99	5.60	0.355	1	

Significance codes: *** < 0.001; ** < 0.01; * < 0.05; . < 0.1

Table D10: Multiple comparisons of means (Tukey contrasts) of the FID (m) of eight focal bird species flushed from different plant species at air temperatures of 35 ^{o}C and above in the Kalahari Desert in October and November 2015, from the model in Table 3: FID ~ (transect) + air temperature + starting distance + time of day + bird species + plant species + location + activity.

Plant species comparisons	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**	**Significance code**
Senegalia mellifera - Boscia albitrunca	-5.30	3.30	-1.607	0.2393	
Vachellia erioloba - Boscia albitrunca	6.90	2.81	2.459	0.0365	*
Vachellia erioloba - Senegalia mellifera	12.20	2.60	4.697	<0.001	***

Significance codes: *** < 0.001; ** < 0.01; * < 0.05; . < 0.1

At air temperatures below 35 ^{o}C

Table D11: Multiple comparisons of means (Tukey contrasts) of the FID (m) of eight focal bird species between different times of day at air temperatures below 35 ^{o}C in the Kalahari Desert in October and November 2015, from Model 1, Table 5: FID ~ (transect) + starting distance + time of day + bird species + plant species + location + exposure + activity.

Time of day comparisons	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**
Early morning - Afternoon	1.55	1.40	1.103	0.512
Late morning - Afternoon	2.32	1.35	1.722	0.197
Late morning - Early morning	0.77	1.30	0.592	0.824

Table D12: Multiple comparisons of means (Tukey contrasts) of FID (m) between eight focal bird species at air temperatures below 35 ^{o}C in the Kalahari Desert in October and November 2015, from Model 1, Table 5: FID ~ (transect) + starting distance + time of day + bird species + plant species + location + exposure + activity.

Bird species comparisons	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**	**Significance code**
Cape Turtle Dove - Black-chested Prinia	8.49	2.82	3.008	0.0503	.
Chestnut-vented Tit-Babbler - Black-chested Prinia	-2.50	2.10	-1.193	0.9288	
Fawn-coloured Lark - Black-chested Prinia	3.26	2.82	1.158	0.9387	
Kalahari Scrub-Robin - Black-chested Prinia	3.95	2.59	1.529	0.7792	
Scaly-feathered Finch - Black-chested Prinia	4.59	2.38	1.926	0.5157	
Sociable Weaver - Black-chested Prinia	6.15	2.75	2.241	0.3123	
Yellow-bellied Eremomela - Black-chested Prinia	1.54	2.13	0.721	0.996	
Chestnut-vented Tit-Babbler - Cape Turtle Dove	-10.99	2.80	-3.93	<0.01	**
Fawn-coloured Lark - Cape Turtle Dove	-5.23	2.33	-2.247	0.3099	
Kalahari Scrub-Robin - Cape Turtle Dove	-4.54	2.45	-1.85	0.5691	
Scaly-feathered Finch - Cape Turtle Dove	-3.90	2.06	-1.892	0.5398	
Sociable Weaver - Cape Turtle Dove	-2.34	2.38	-0.981	0.975	
Yellow-bellied Eremomela - Cape Turtle Dove	-6.95	2.89	-2.408	0.2252	
Fawn-coloured Lark - Chestnut-vented Tit-Babbler	5.77	2.92	1.975	0.482	
Kalahari Scrub-Robin - Chestnut-vented Tit-Babbler	6.46	2.71	2.384	0.2372	
Scaly-feathered Finch - Chestnut-vented Tit-Babbler	7.10	2.50	2.843	0.0794	.
Sociable Weaver - Chestnut-vented Tit-Babbler	8.66	2.80	3.097	0.0387	*
Yellow-bellied Eremomela - Chestnut-vented Tit-Babbler	4.04	2.14	1.885	0.5445	
Kalahari Scrub-Robin - Fawn-coloured Lark	0.69	2.36	0.294	1	
Scaly-feathered Finch - Fawn-coloured Lark	1.33	2.08	0.639	0.9981	
Sociable Weaver - Fawn-coloured Lark	2.89	2.43	1.19	0.9296	
Yellow-bellied Eremomela - Fawn-coloured Lark	-1.72	2.96	-0.583	0.999	
Scaly-feathered Finch - Kalahari Scrub-Robin	0.64	2.10	0.304	1	
Sociable Weaver - Kalahari Scrub-Robin	2.20	2.49	0.885	0.9862	
Yellow-bellied Eremomela - Kalahari Scrub-Robin	-2.41	2.75	-0.878	0.9868	
Sociable Weaver - Scaly-feathered Finch	1.56	2.07	0.752	0.9948	
Yellow-bellied Eremomela - Scaly-feathered Finch	-3.05	2.56	-1.194	0.9283	
Yellow-bellied Eremomela - Sociable Weaver	-4.62	2.83	-1.633	0.7156	

Significance codes: *** < 0.001; ** < 0.01; * < 0.05; . < 0.1

Table D13: Multiple comparisons of means (Tukey contrasts) of the FID (m) of eight focal bird species flushed from different plants at air temperatures below 35 ^{o}C in the Kalahari Desert in October and November 2015, from Model 1, Table 5: FID ~ (transect) + starting distance + time of day + bird species + plant species + location + exposure + activity.

Plant species comparisons	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**	**Significance code**
Boscia albitrunca - Open ground	-0.38	2.54	-0.151	1	
Dead tree - Open ground	-1.37	4.84	-0.283	0.9997	
Rhigozum trichotomum - Open ground	4.15	3.45	1.204	0.8134	
Senegalia mellifera - Open ground	-2.58	2.26	-1.141	0.8451	
Vachellia erioloba - Open ground	1.08	2.27	0.474	0.9964	
Dead tree - *Boscia albitrunca*	-0.99	4.73	-0.209	0.9999	
Rhigozum trichotomum - Boscia albitrunca	4.54	3.30	1.375	0.7134	
Senegalia mellifera - Boscia albitrunca	-2.19	2.01	-1.09	0.8689	
Vachellia erioloba - Boscia albitrunca	1.46	1.93	0.757	0.9699	
Rhigozum trichotomum - Dead tree	5.52	5.04	1.097	0.8658	
Senegalia mellifera - Dead tree	-1.21	4.47	-0.27	0.9998	
Vachellia erioloba - Dead tree	2.45	4.46	0.549	0.9929	
Senegalia mellifera - Rhigozum trichotomum	-6.73	2.83	-2.378	0.1428	
Vachellia erioloba - Rhigozum trichotomum	-3.08	2.92	-1.055	0.8841	
Vachellia erioloba - Senegalia mellifera	3.65	1.29	2.835	0.0441	*

Significance codes: *** < 0.001; ** < 0.01; * < 0.05; . < 0.1

Table D14: Multiple comparisons of means (Tukey contrasts) of the FID (m) of eight focal bird species flushed from different locations at air temperatures below 35 ^{o}C in the Kalahari Desert in October and November 2015, from Model 1, Table 5: FID ~ (transect) + starting distance + time of day + bird species + plant species + location + exposure + activity.

Bird location comparisons	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**
Dead Tree - Canopy	11.03	5.44	2.028	0.157
Ground - Canopy	2.50	2.10	1.19	0.603
Tree Top - Canopy	1.61	1.87	0.859	0.807
Ground - Dead Tree	-8.52	5.81	-1.467	0.425
Tree Top - Dead Tree	-9.42	5.21	-1.807	0.243
Tree Top - Ground	-0.90	2.58	-0.347	0.984

Black-bulb analyses

In the shade

Table D15: Multiple comparisons of means (Tukey contrasts) of black-bulb temperature (°C) in the shade of different plant species in the Kalahari Desert in October and November 2015. Model: Black-bulb temperature ~ plant species.

Plant species comparisons	**Estimate**	**Std. Error**	**t value**	**Pr(>|t|)**	**Significance code**
Senegalia mellifera - Boscia albitrunca	2.83	0.20	14.1	< 0.001	***
Vachellia erioloba - Boscia albitrunca	0.96	0.20	4.787	< 0.001	***
Vachellia erioloba - Senegalia mellifera	-1.87	0.20	-9.316	< 0.001	***

Significance codes: *** < 0.001; ** < 0.01; * < 0.05; . < 0.1

In the sun

Table D16: Multiple comparisons of means (Tukey contrasts) of black-bulb temperature (°C) in the sun in different placements (*Boscia albitrunca* vs *Senegalia mellifera* vs *Vachellia erioloba* vs dead tree vs open ground) in the Kalahari Desert in October and November 2015. Model: Black-bulb temperature ~ placement.

Placement comparisons	**Estimate**	**Std. Error**	**t value**	**Pr(>|t|)**	**Significance code**
Dead tree - *Boscia albitrunca*	-2.75	0.29	-9.434	< 0.001	***
Open ground - *Boscia albitrunca*	3.03	0.29	10.402	< 0.001	***
Senegalia mellifera - Boscia albitrunca	-0.80	0.29	-2.726	0.0503	.
Vachellia erioloba - Boscia albitrunca	-2.47	0.29	-8.46	< 0.001	***
Open ground - Dead tree	5.78	0.29	19.824	< 0.001	***
Senegalia mellifera - Dead tree	1.96	0.29	6.703	< 0.001	***
Vachellia erioloba - Dead tree	0.29	0.29	0.979	0.8649	
Senegalia mellifera - Open ground	-3.83	0.29	-13.121	< 0.001	***
Vachellia erioloba - Open ground	-5.50	0.29	-18.857	< 0.001	***
Vachellia erioloba - Senegalia mellifera	-1.67	0.29	-5.728	< 0.001	***

Significance codes: *** < 0.001; ** < 0.01; * < 0.05; . < 0.1

Appendix E – Species-specific models of FID for eight Kalahari bird species

Table E1: A summary of the effect of each explanatory variable on FID (m) for Black-chested Prinia, based on the best-fit model of FID for this species (from Table 7). This model includes starting distance, plant species (reference variable: *Rhigozum trichotomum*), time of day (reference variable: afternoon), exposure (reference variable: shade) and location (reference variable: canopy).

Variable	**Estimate**	**Std. Error**	**t value**
Intercept	5.38	4.43	1.214
Starting distance	0.30	0.10	2.92
Plant species: *Senegalia mellifera*	-5.21	2.96	-1.758
Plant species: *Vachellia erioloba*	-1.68	3.18	-0.528
Time of day: Early morning	3.51	2.61	1.346
Time of day: Late morning	4.26	2.46	1.731
Exposure: Sun	1.09	2.31	0.474
Location: Tree top	4.89	3.10	1.575

Table E2: A summary of the effect of each explanatory variable on FID (m) for Cape Turtle Dove, based on the best-fit model of FID for this species (from Table 7). This model includes starting distance, plant species (reference variable: no plant, i.e. open ground), time of day (reference variable: afternoon), activity (reference variable: mobile), exposure (reference variable: shade) and location (reference variable: canopy).

Variable	**Estimate**	**Std. Error**	**t value**
Intercept	-4.57	10.70	-0.427
Starting distance	0.71	0.11	6.479
Plant species: *Boscia albitrunca*	9.23	5.45	1.694
Plant species: *Vachellia erioloba*	7.06	6.18	1.142
Time of day: Early morning	-6.37	5.32	-1.199
Time of day: Late morning	-5.19	4.12	-1.259
Activity: Stationary	-2.07	5.30	-0.391
Exposure: Sun	4.72	6.60	0.715
Location: Ground	1.03	5.81	0.177

Table E3: A summary of the effect of each explanatory variable on FID (m) for Chestnut-vented Tit-Babbler, based on the best-fit model of FID for this species (from Table 7). This model includes starting distance, plant species (reference variable: *Boscia albitrunca*) and time of day (reference variable: afternoon).

Variable	**Estimate**	**Std. Error**	**t value**
Intercept	10.64	4.54	2.345
Starting distance	0.32	0.09	3.368
Plant species: *Senegalia mellifera*	-8.10	3.49	-2.318
Plant species: *Vachellia erioloba*	-3.57	3.25	-1.099
Time of day: Early morning	-1.46	2.87	-0.51
Time of day: Late morning	-4.37	2.87	-1.521

Table E4: A summary of the effect of each explanatory variable on FID (m) for Fawn-coloured Lark, based on the best-fit model of FID for this species (from Table 7). This model includes starting distance, plant species (reference variable: no plant, i.e. open ground), time of day (reference variable: afternoon), activity (reference variable: mobile), exposure (reference variable: shade) and location (reference variable: ground).

Variable	**Estimate**	**Std. Error**	**t value**
Intercept	7.16	4.34	1.649
Starting distance	0.45	0.08	5.599
Plant species: Dead tree	-7.19	6.04	-1.189
Plant species: *Senegalia mellifera*	-7.70	3.45	-2.235
Plant species: *Vachellia erioloba*	1.64	3.56	0.46
Time of day: Early morning	-0.09	4.45	-0.021
Time of day: Late morning	4.99	2.34	2.129
Activity: Stationary	-2.96	2.58	-1.15
Exposure: Sun	2.60	4.76	0.546
Location: Tree top	0.02	5.93	0.003

Table E5: A summary of the effect of each explanatory variable on FID (m) for Kalahari Scrub-Robin, based on the best-fit model of FID for this species (from Table 7). This model includes starting distance, plant species (reference variable: no plant, i.e. open ground), time of day (reference variable: afternoon), activity (reference variable: mobile), exposure (reference variable: shade) and location (reference variable: canopy).

Variable	**Estimate**	**Std. Error**	**t value**
Intercept	-1.43	8.26	-0.173
Starting distance	0.58	0.12	4.898
Plant species: *Senegalia mellifera*	1.07	6.09	0.176
Plant species: *Vachellia erioloba*	11.93	6.63	1.801
Time of day: Early morning	4.78	6.43	0.744
Time of day: Late morning	4.66	4.45	1.047
Activity: Stationary	-7.36	5.35	-1.378
Exposure: Sun	4.01	5.82	0.688
Location: Ground	-4.44	5.99	-0.742

Table E6: A summary of the effect of each explanatory variable on FID (m) for Scaly-feathered Finch, based on the best-fit model of FID for this species (from Table 7). This model includes starting distance, plant species (reference variable: no plant, i.e. open ground), time of day (reference variable: afternoon), activity (reference variable: mobile), exposure (reference variable: shade) and location (reference variable: canopy).

Variable	**Estimate**	**Std. Error**	**t value**
Intercept	-4.78	7.14	-0.67
Starting distance	0.46	0.08	5.663
Plant species: *Boscia albitrunca*	5.54	6.19	0.894
Plant species: *Rhigozum trichotomum*	10.68	8.02	1.332
Plant species: *Senegalia mellifera*	0.29	5.27	0.054
Plant species: *Vachellia erioloba*	3.60	5.48	0.658
Time of day: Early morning	0.82	3.08	0.267
Time of day: Late morning	-0.70	2.80	-0.25
Activity: Stationary	2.01	4.60	0.438
Exposure: Sun	4.82	3.95	1.219
Location: Ground	12.01	5.03	2.387
Location: Tree top	3.52	4.23	0.831

Table E7: A summary of the effect of each explanatory variable on FID (m) for Sociable Weaver, based on the best-fit model of FID for this species (from Table 7). This model includes starting distance, plant species (reference variable: no plant, i.e. open ground), time of day (reference variable: afternoon), activity (reference variable: mobile), exposure (reference variable: shade) and location (reference variable: canopy).

Variable	**Estimate**	**Std. Error**	**t value**
Intercept	3.87	8.93	0.433
Starting distance	0.54	0.09	5.822
Plant species: *Boscia albitrunca*	-10.03	7.11	-1.411
Plant species: *Senegalia mellifera*	-9.83	6.23	-1.578
Plant species: *Vachellia erioloba*	-5.88	6.05	-0.971
Time of day: Early morning	3.56	3.47	1.026
Time of day: Late morning	7.89	3.72	2.123
Activity: Stationary	-3.71	4.55	-0.815
Exposure: Sun	3.13	4.90	0.638
Location: Ground	3.82	5.42	0.706
Location: Tree top	9.66	5.33	1.811

Table E8: A summary of the effect of each explanatory variable on FID (m) for Yellow-bellied Eremomela, based on the best-fit model of FID for this species (from Table 7). This model includes plant species (reference variable: *Boscia albitrunca*), time of day (reference variable: afternoon), exposure (reference variable: shade) and location (reference variable: canopy).

Variable	**Estimate**	**Std. Error**	**t value**
Intercept	13.27	4.39	3.021
Plant species: *Senegalia mellifera*	9.06	4.15	2.18
Plant species: *Vachellia erioloba*	6.15	4.12	1.492
Time of day: Early morning	-0.89	3.26	-0.272
Time of day: Late morning	2.04	3.21	0.637
Exposure: Sun	9.07	4.37	2.077
Location: Tree top	-13.45	4.99	-2.694