Handling the heat: keeping water available for birds of the Tankwa Karoo Desert

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Submitted in partial fulfilment of the requirements for the degree of Master of Science in Conservation Biology by coursework and dissertation

August 2022

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Acknowledgements

Firstly, I would like to thank my supervisory team: Dr. Susan Cunningham, Dr. Nicola Van Wilgen, Dr. Alan Lee and Dr. Wendy Foden for their support and input throughout this thesis, and for always finding time to address my drafts and queries despite their very busy schedules. I would also like to say a very special thank you to my main supervisor Dr. Susan Cunningham for her unwavering support, helpful experience and vast knowledge which provided direction every step of the way. I would also like to extend my appreciation to the support staff of the FitzPatrick Institute and Biological Sciences department, notably Mr Calvan Hartnick for his assistance in designing the shade structures.

I extend my gratitude to the WWF Wildlife Adaptation Innovation Fund for providing the grant that funded this research (grant number: CM11640) and to Dr. Nikhil Advani for his support on this project, as well as for his company and assistance in the field. I would like to thank and acknowledge SANParks for providing accommodation in the Tankwa Karoo National Park (TKNP) during data collection in January and February 2022. I am especially grateful to all the SANParks staff at the TKNP for their hospitality, support, input and assistance during this time. Furthermore, I would like to thank and acknowledge the South African Weather Service (SAWS) for providing long term temperature and precipitation data that was included in this thesis.

A special thank you goes to all the staff at the Tankwa Tented Camp for their hospitality, refreshing company and the much-needed respite from the heat (including multiple tyre repairs and the occasional cold beer). I express my gratitude to Gideon De Wet and Grant Smith of the SANParks Table Mountain Honarary Rangers, and to Johanna Hawker and Emma Wright of the Conservation Biology Masters 2021/2 cohort, for their field assistance and great company which never wavered even during the long days walking in the heat. Here I would like to extend this thank you to the entire CB Masters class without whom the past year would have been a far more grueling affair, and a special thank you goes to Sara Forsberg for ensuring I remained fed in the final days of this thesis.

Finally, I would like to thank my family and friends for their unwavering support in all aspects of my life, without whom very little would be possible.

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Abstract

Climate change poses one of the biggest risks to biodiversity globally. Africa is warming at twice the global average rate and African bird species are therefore at risk, particularly in desert environments where they are already operating near physiological limits. Desert air temperatures in the subtropical latitudes will rise by 3°-5°C by the end of the century. When air temperatures are higher than body temperature, birds must use evaporative cooling to avoid hyperthermia. However, evaporative cooling requires water and a tradeoff exists between hyperthermia and dehydration. For drinking species which need open water sources in order to rehydrate, this tradeoff is exacerbated by high operative temperatures on the ground near the water's edge during periods of extreme heat. This study assessed whether providing artificial shade at waterholes can buffer impacts of high temperature by increasing accessibility of water to birds, potentially facilitating persistence of desert bird communities under climate change. I used a before-after control-impact experimental design to test the impact of shade provision on visitation rates, species richness and the timing of visits by desert birds to waterholes in the Tankwa Karoo National Park of South Africa. Providing shade reduced afternoon waterside operative temperatures below lethal limits for many small passerine species and successfully buffered birds' visitation rates to the water's edge during hot periods, although species richness did not change. Overall bird visitation rates to waterholes increased in the afternoon relative to control sites in response to the addition of shade but decreased in the morning, likely due to a perceived/actual predation risk while operative temperatures were low and shade structures provided no thermal benefit. Responses to shade were species-specific, with the overall positive response driven in part by two common species: Grey-backed Sparrow-larks *Eremopterix verticalis* and Tractrac Chats *Emarginata tractrac*. Two species (Cape Sparrows *Passer melanurus* and White-throated Canaries *Crithagra albogularis*) responded negatively to the provision of shade. There was an observed shift in bird visitation rates from the morning to the afternoon at shaded structures, suggesting temperature as a primary driver in the use of shade. As temperatures increase under climate change, birds may be forced to drink more in the afternoon due to rising water demands for thermoregulation. Shade structures such as those trialed in this study may have the potential to facilitate this shift and keep water accessible to desert birds in the face of temperature increases.

Introduction

Climate change poses one of the greatest threats to biodiversity globally (Nunez *et al.,* 2019; Suárez *et al.,* 2002). According to the latest IPCC report (2022) between 14% and 48% of assessed species face high risk of extinction under current global warming scenarios. Africa is expected to warm at twice the global rate (Engelbrecht *et al.,* 2015) and is expected to experience an increase in the frequency and temperature of heatwaves (Mbokodo *et al.,* 2020), coupled with more erratic precipitation (Georgi & Bi, 2005). IPCC models also suggest that deserts in the subtropical latitudes will increase in average maximum temperature by 3°-5° C before the end of the century (IPCC, 2007,2011,2022). African species are therefore at risk, particularly in desert environments where they are already operating near their physiological limits (Archer & Predick, 2008; Iknayan & Beissinger, 2018; Schmidt-Nielson, 1964). Desert biota are often highly specialized and have high levels of endemism (Maggs *et al.,* 1998; Major, 1988; Van der Merwer *et al.,* 2015). Desert ecosystems and the species within them are therefore vulnerable to changes in temperature and rainfall which not only threaten them physiologically, but also affect their habitat and basic resource acquisition (Iknayan and Beissinger, 2018). These changes are often associated with range shifts, catastrophic mortality events or even community collapses (Albright *et al.,* 2017; Conradie *et al.,* 2019, 2020; Iknayan & Beissinger, 2018: McKechnie & Wolf, 2010, 2019; McKechnie *et al.,* 2012). Finding management interventions to mitigate such impacts is therefore crucial.

Organisms in desert environments are adapted to cope with temperature extremes through physiological and behavioral means (Davies, 1982; Dean & Williams, 2004; McKechnie & Wolf, 2019; Schmidt-Nielson, 1964). Behaviourally, desert species may handle extreme heat by being nocturnal, making use of thermal refugia and through shade seeking (Dean & Williams, 2004; Schmidt-Nielson, 1964; Randall, 1993; Ruth *et al.,* 2020). Diurnal organisms, like some small mammals and reptiles, will often make use of underground burrows during the hottest parts of the day (Levy *et al.,* 2016; Moore *et al.,* 2018). Some diurnal rodents will choose to avoid high temperatures and dehydration by sheltering in burrows, even when high quality forage is available (Levy *et al.,* 2016). Most bird species are diurnal, including desert passerines, and rarely make use of burrows (Dean & Williams, 2004; Fisher *et al.,* 1972). They will, however, make use of thermal refugia in their environment, access available water to bathe when it is hot, change activity patterns to cooler times of the day, and/or adopt a more nomadic lifestyle (Dean & Williams, 2004; Lee *et al.,* 2017; Ruth *et al.,* 2020). Zebra Finches (*Taeniopygia castanotis*), for example, will forage and drink earlier in the day in preparation for hotter periods during which they avoid sun exposure (Cooper *et al.,* 2019).

Avoiding the heat is not always possible for desert birds and higher temperatures due to climate change will only exacerbate the risk of hyperthermia and the need for thermoregulation. Southern Pied Babblers (*Turdoides bicolor*) in the Kalahari Desert, for example, reduced foraging efficiency due to thermoregulatory needs such as panting (du Plessis *et al.,* 2012). Du Plessis *et al.,* (2012) found that increased temperatures led to increased thermoregulatory demands which in turn led to a decrease in body condition, findings consistent with other studies in the same habitat (Conradie *et al*., 2019; Van de Ven *et al*., 2019). Foraging requirements may force birds to endure hotter temperatures to maintain physical condition (Conradie *et al.,* 2019; Kemp *et al.,* 2020; Van de Ven *et al*., 2019), and higher temperatures due to climate change will only exacerbate the risk of hyperthermia and the need for thermoregulation.

Desert air temperatures regularly exceed avian body temperatures (~40-42°C). Increases in temperature and the frequency of heatwaves due to climate change mean birds will be increasingly exposed to potentially lethal temperatures in desert environments (Conradie *et al.,* 2019, 2020; McKechnie *et al.,* 2021; McKechnie & Wolf, 2019). Studies conducted on thermal tolerance under laboratory conditions in South Africa, Australia and the United States suggest desert passerines reach their upper limits of air temperature tolerance at around 46-54°C (McKechnie *et al.,* 2021; McKechnie & Wolf, 2019). Operative temperatures (environmental temperatures experienced by organisms incorporating solar radiation, air temperature and other environmental factors) in full sun, may exceed 60°C in many desert environments (Wolf & Walsberg, 1996a; McKechnie *et al.,* 2021). This means that desert birds are regularly exposed to potentially harmful temperatures. Small passerine species are particularly at risk as smaller organisms have a higher surface area to body ratio, making them more susceptible to temperature changes (McKechnie *et al.,* 2012, 2021; Walsberg, 1993). Wolf and Walsberg (1996a) found that *Auriparus flaviceps,* a small passerine species, may experience up to a 12°C increase in operative temperature when moving from a shaded perch to full sun. Heat exposure is therefore a concerning and potentially lethal threat to the persistence of avian communities in arid environments. Physiological methods of thermoregulation therefore become more important when high temperatures and sun exposure cannot be avoided (Albright *et al.,* 2017; Conradie *et al.,* 2020; McKechnie & Wolf, 2010, 2019; Mckechnie *et al.,* 2012).

Evaporative-cooling is an important mechanism through which birds are able to thermoregulate when air temperatures exceed body temperature (McKechnie *et al.,* 2012, 2021; McKechnie & Wolf, 2019; Smith *et al.,* 2017; Walsberg, 1993; Whitfield *et al.,* 2015; Wolf & Walsberg, 1996b). In many arid areas, vegetation is extremely sparse and thermal refugia are few and far between. Evaporative cooling is therefore a primary method through which birds are able to control their body temperature and avoid lethal limits (Albright *et al.,* 2017; Conradie *et al.,* 2019; Dean & Williams, 2004; McKechnie *et al.,* 2012, 2021). However, evaporative cooling comes with a high water cost (McKechnie & Wolf, 2010; McKechnie *et al.,* 2012, 2021). Replenishing water is therefore important in ensuring individual survival and species persistence in many desert passerines (McKechnie and Wolf 2010; Albright *et al.,* 2017). This tradeoff means that birds are required to balance water requirements and heat pressures and therefore have to risk potentially lethal dehydration when avoiding the equally detrimental effects of hyperthermia (Conradie *et al.,* 2019; Fisher *et al.,* 1972; Lee *et al.,* 2017; McKechnie & Wolf, 2010; McKechnie et al., 2012, 2021). Whitfield *et al.* (2015) suggest that evaporative water loss increases linearly as air temperatures approach avian body temperature while McKechnie & Wolf (2010) suggest that in arid hot environments under current global warming predictions, water requirements will increase by 150-200%. Albright *et al.* (2017) suggest a similar trend in songbirds in the USA, showing that the increase in temperature could quadruple the risk of lethal dehydration in smaller birds.

Studies conducted in the deserts of South Africa have shown that ~45% of bird species in these environments rely on surface water for drinking (Lee *et al.,* 2019) and that even those species that are not obligate drinkers (i.e. those that can obtain all their water from food) tend to make use of water during extreme temperature events (Abdu *et al*., 2018b; Harrison *et al.,* 1997; Smit *et al*., 2019). Surface water and its relative accessibility are therefore important factors shaping avian communities in desert environments (Abdu *et al.,* 2018a; Fisher *et al*., 1972; Lee & Write, 2020; Lee *et al.,* 2017). Abdu *et al*. (2018a) showed that the species richness and density of desert birds were directly influenced by the presence of surface water. This is consistent with Fisher *et al.* (1972) who suggested that a species' success was related to the ability to locate and use surface water in desert environments. Granivorous species tend to drink more than insectivores (insects have a higher water content) and increase their water intake with an increase in temperature (Abdu *et al.,* 2018b; Bartholomew & Cade, 1963; Harrison *et al.,* 1997; Lee *et al.,* 2017; MacMillen & Baudinette, 1993; MacMillen, 1990; Smit *et al.,* 2019). It is apparent that many species in hot and dry climates are heavily reliant on surface water to alleviate dehydration caused by evaporative water loss for thermoregulation. Surface water is therefore likely to become increasingly important as temperatures continue to rise as a result of climate change.

Several factors influence the accessibility of surface water for desert bird communities. Direct effects of changing weather patterns such as reduced precipitation and increased temperatures are expected to reduce water availability. At the individual level, birds also tradeoff energy demands of locating and accessing water against hydration needs (Fisher *et al.,* 1972). Some species like sandgrouse (*Pteroclid* species), for example, travel vast distances, expending considerable energy to locate water in arid environments (Maclean, 1983, 1996). Tradeoffs also exist with regards to predation risk due to the tendency of desert predators to congregate around waterholes (Cade, 1965; Ferns & Hinsley, 1995; Fisher *et al.,* 1972).

While the above trade-offs may influence the accessibility of waterholes in an environment, water, when present and devoid of predators, may still be unavailable. This is because the area surrounding surface water may become too hot to access without risking lethal hyperthermia. Waterholes are often surrounded by bare ground (known as piospheres) due to foraging and trampling by large mammals (James *et al.,* 1999). In arid areas, vegetation is already sparse and water sources are often exposed to full sun. Operative temperatures in piospheres, like any area exposed to direct sunlight, are thus far higher than air temperatures (Orolowitz, 2020; Wolf & Walsberg, 1996a). Orolowitz (2020) found that operative temperatures approached 60°C on the ground in direct sunlight in the Tankwa Karoo National Park (TKNP), South Africa. Birds making use of surface water in areas like the TKNP are therefore likely to be exposed to temperatures far above their body temperature particularly if attempting to drink during the warmest hours of the day. Accessing water is likely to expose birds to operative temperatures above their thermal limits, meaning that in an attempt to replenish water and avoid dehydration, birds may be risking lethal hyperthermia, leaving them vulnerable to extreme heat events and global temperature increases.

Studies of bird communities in arid areas and their water needs have suggested that keeping surface water available and providing thermal refugia are potential ways to facilitate adaptation to climate change (Abdu *et al.,* 2018b; Albright *et al.,* 2017). Recent research on the collapse of avian communities has confirmed that there is a strong relationship between decreased precipitation and a decrease in species richness in the Mojave desert (Iknayan & Beissinger, 2018). This could be attributed to the inability of many species to meet the water demands placed on them by evaporative-cooling (Riddell *et al.,* 2019) and is consistent with further findings by Iknayan & Beissinger (2018) that the presence of surface water partially buffered the community collapses at a local scale. Providing thermal refugia at waterholes by shading the edges of surface water may therefore reduce the thermal restrictions of high operative temperature surrounding water sources and buffer negative effects of climate change.

Abdu *et al.,* (2018b) explored the use of shade structures over artificial waterholes in the Kalahari desert for this very purpose and found that providing shade at some waterholes increased the visitation rates of small passerines. They also found that the timing of visitations by these smaller passerines changed; with more visitations to shaded waterholes during the hotter periods of the day (Abdu *et al.,* 2018b). This confirms the potential benefits of providing artificial shade, allowing smaller birds to access water sources throughout the day. Unfortunately Abdu *et al.* (2018b) also found that some dove, weaver and sparrow species (all larger species than those that responded positively) reduced their visitation rates to shaded waterholes. They proposed that the shader design may be causing a percieved predation risk and that changing the design to be more sensitive to the needs of several species, not shading the entire waterhole, and blending the structure into the landscape would be important factors to explore in future research (Abdu *et al.,* 2018b). Temperature in the Kalahari was also limiting and did not exceed avian body temperature for the duration of the study (Abdu *et al.*, 2018b). Arid parts of the Karoo provide both high temperatures (Van Der Merwe *et al.,* 2015) and are rich in avifauna, albiet at lower densities than the Kalahari (Dean, 1995). Up to 400 species have been recorded in the Karoo and half that number are considered typical of the biome (Dean, 1995; Lee & Wright, 2020). Lee & Wright (2020) found that the presence of surface water in the Karoo was associated with high species richness at a fine scale and waterholes in the more arid parts of the Karoo may therefore provide the ideal site for further study.

This study aimed to understand whether providing shade at waterholes could buffer the impacts of high temperature by increasing accessibility of water to birds, and to understand the potential of providing artificial shade at the water's edge as a mechanism for facilitating adaptation by desert bird communities in light of current climate change predictions. This study also aimed to pilot a different shade structure design to meet the suggested specifications discussed by Abdu *et al.* (2018b), in the even more arid Tankwa Karoo National Park. The objectives were:

1.) To assess the impact of the provision of artificial shade on operative temperatures at the water's edge
2.) To assess the impact of shade structures on bird visitation rates both overall (all species combined) and for individual species.
3.) To assess the impact of shade structures on the species richness and composition of the bird community accessing waterholes in the TKNP.
4.) To assess the impact shade structures have on the timing of visits by birds to waterholes.

I predicted that shade structures would significantly reduce operative temperatures at the water's edge in the afternoon. I also predicted that the frequency of visitation by small passerines would increase at shaded waterholes and that visitation rates would increase during the hottest parts of the day. Furthermore I predicted that more bird species would make use of shaded waterholes than unshaded waterholes, and that there would be a shift in the timing of visitation from the morning to the afternoon at shaded structures.

Methods and materials

Study site

This study was conducted in January-February 2022 in the Tankwa Karoo National Park (TKNP) in South Africa's Northern Cape province (32.241° S, 20.096° E; Figure 1). The TKNP was established in 1986 (Rubin, 1998) and covers roughly 145 000 ha of the Tanqua Karoo (SANParks, 2014). The Tanqua Karoo (and by extension TKNP) is located within the Succulent Karoo biome which is one of only two arid regions in the world categorized as global biodiversity hotspots (Desmet *et al.,* 2002; Conservation International, 2013). As such, the park is home to an array of species, including 187 bird species (SANParks, 2022), 10 of which are endemic to the Karoo biome (Lee & Wright, 2020). The topography of the park varies dramatically. The steep geographical gradient is characterized by a mixture of low-lying plains interspersed with isolated hills, bordered by the Cederberg mountains to the west, the Elandsberg mountains to the north and the Roggeveld escarpment to the east/northeast (Steyn *et al.,* 2013; Park Management Plan, 2014). This, together with the underlying geomorphology, have resulted in a multitude of microhabitats and vegetation types (Steyn *et al.,* 2013). Van Der Merwe *et al.* (2015) described 13 landscape units for the TKNP to be used to inform management action. These landscape units have been used in this study as a proxy for vegetation and by extension, habitat type (Figure 1). Water in the park is limited to a few man-made water points, a number of natural springs and isolated temporary pools in the predominantly dry Tankwa River bed (depending on precipitation).

The TKNP is one of the most arid regions of the Succulent Karoo biome, typically receiving 0-200mm of rain per year (Van Der Merwe *et al.,* 2015). Rainfall occurs throughout the year though the majority falls during the winter months between May and August (Park Management Plan, 2014). The mean maximum summer temperature annually recorded in the park over a seven-year period is 38.4°C (Van Der Merwe *et al.,* 2015) with a maximum recorded temperature of 50°C (SANParks, 2022). Temperatures are highest between November and March and typically peak in January and February (Park Management Plan, 2014). Air temperature, precipitation, wind speed and wind direction during the study period were measured at 30-minute intervals using a portable weather station (Vantage Pro2, Davis Instruments, Hayward, CA) located at the SANParks Roodewerf reception (32.24108°S, 20.09569°E).

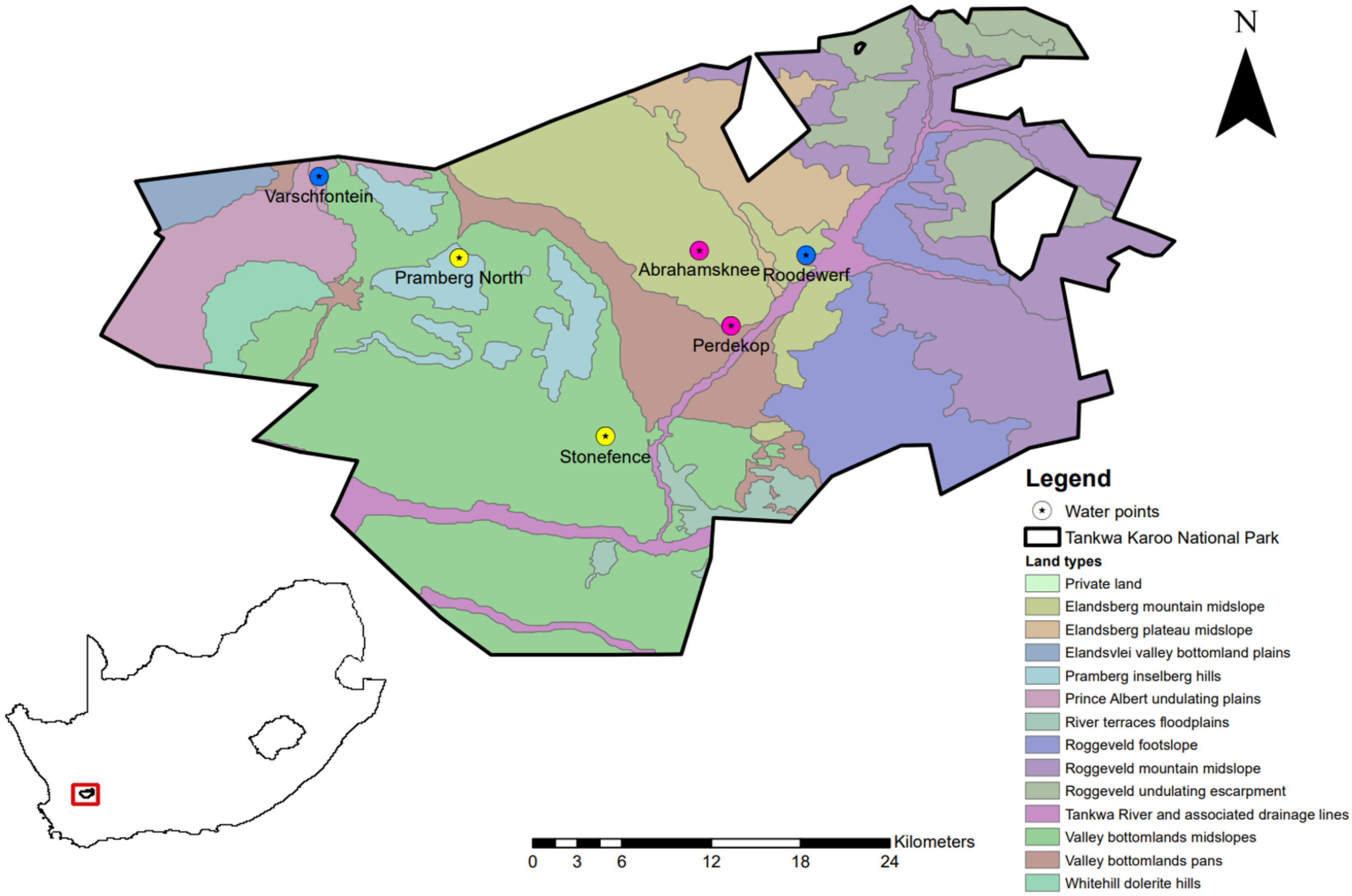


Figure 1: Study site and six selected waterholes paired by colour based on similarity of habitat, waterhole characteristics (natural or artificial) and access considerations in the Tankwa Karoo National Park, overlain on the 13 landscape units used as a proxy for vegetation type as described by Van Der Merwe *et al.* (2015). Map insert shows the position of the Tankwa Karoo National Park within South Africa.

Experimental design

A ‘before-after control-impact’ (BACI) experiment (Green, 1979; Skalski & Robson, 2012; Abdu *et al.,* 2018a) was used to assess impacts of providing shade at waterholes on (1) operative temperature at the water’s edge (2) bird visitation rates to water, (3) species richness and community composition of the bird community using waterholes, and (4) timing of bird visits, during the hottest time of year. A BACI design rather than fully-balanced design was chosen due to time constraints related to receding water levels and peak warm temperatures in the area.

This experiment consisted of two phases, a ‘before’ phase (Phase 1) during which waterholes received no artificial shade and baseline data on bird visitation rates were collected, and an ‘after’ phase (Phase 2) during which half the waterholes received artificial shade and further bird visitation data were collected. This design allowed me to assess any significant interaction between waterhole treatment i.e., ‘Control’ (unshaded waterholes) or ‘Experimental’ (shade-provided), and phase (‘Phase 1’ before shade was provided at ‘Experimental’ waterholes, and ‘Phase 2’ after shading). That is, I could infer if changes in bird visitation rates were likely due to the impact itself (provision of shade at ‘Experimental’ waterholes during Phase 2), rather than a result of background effects such as changes in temperature, precipitation or bird density in the TKNP that should affect all waterholes equally. For this study, six waterholes (two natural springs: ‘Stonefence’ and ‘Pramberg North’; and four artificial waterholes: ‘Varschfontein’, ‘Roodewerf’, ‘Abrahamsknee’ and ‘Perdekop’) were selected based on vegetation and landscape type (Figure 1), access considerations (including road conditions and mileage constraints), and whether the water source was likely to last throughout the hot months of January and February. Waterholes were then paired based on landscape type (Figure 1), waterhole type (natural or artificial), surrounding vegetation structure, and our initial assessment of the species and number of birds using them. One of each pair was then randomly assigned to ‘Control’ and ‘Experimental’ treatments. ‘Control’ waterholes were; Stonefence, Perdekop and Roodewerf, while ‘Experimental’ waterholes were; Pramberg North, Abrahamsknee and Varschfontein (Figure 1).

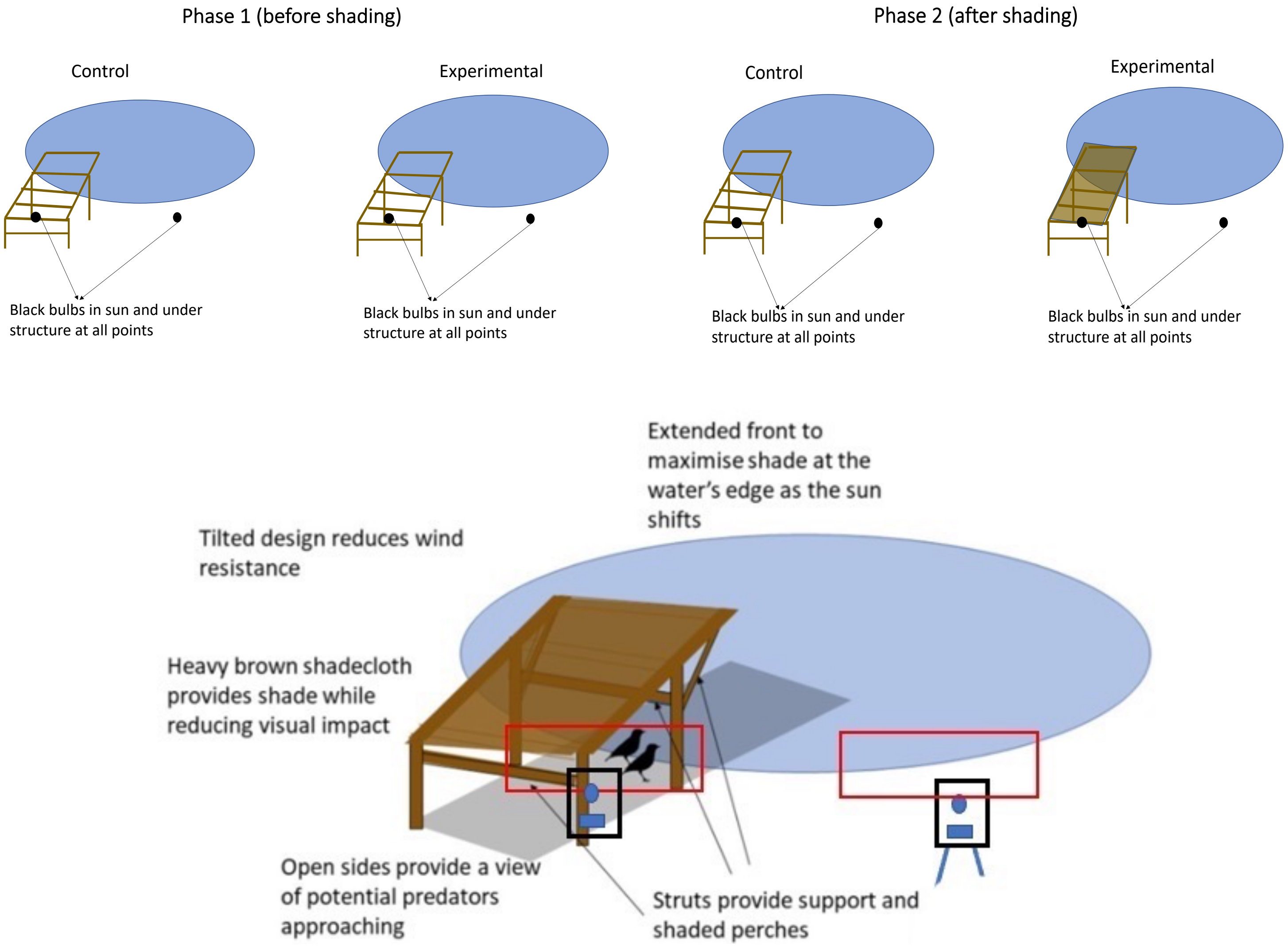


Figure 2: Experimental design showing the Phase 1 ‘before’ and Phase 2 ‘after’ at control and experimental waterholes as well as the ‘open bank’ and ‘structure’ cameras placed at all waterholes (control and experimental) in both phases. The red rectangle indicates the stretches of bank of equivalent size observed by each camera.

Shade structure design and placement

Prior to the beginning of Phase 1, I erected an empty (without shade cloth) shade structure at each of the six waterholes (structures were placed at both 'Control' and 'Experimental' waterholes to ensure the experiment tested the impact of providing shade, rather than the impact of providing a structure; Figure 2). Structures were 2m x 1.25m with 1m front legs and 0.7m back legs (Figure 3) and were constructed using 38mm x 38mm x 3m pine timber battens, 70-inch wood screws, metal stakes for anchorage and heavy-duty cable ties. The angle created by having shorter back legs maximized the shade cast over the water's edge while minimizing resistance to the prevailing wind (Figure 2 & 3). At each waterhole, the structures were placed with the back facing west-north-west to west (between 270° and 300°) depending on what the topography of the waterhole allowed. This was done to ensure the shadow was cast over the water's edge during the afternoon, and provided shade at the water during the hottest part of the day (the shade cast by shade structures reached the waters' edge between 12:00- 12:30 pm during Phase 2 at Experimental waterholes, and these remained shaded until near sunset). The front legs of the structure were secured to metal stakes on average 0.4m from the water's edge.

Structures were erected between the 12th and 14th of January 2022 followed by a habituation period of no data collection up until the 20th January. Phase 1 then took place from the 20th – 31st of January. Heavy duty beige shade cloth (Alnet 90% UV ray block, 'Savannah Gold') was then added to the structures at experimental waterholes between the 31st of January and the 1st of February (Figure 3). Color selection was made as per SANParks specifications, and to blend the structures into the landscape. Shade cloth was secured with wire and wood staples to limit the potential for cloth to move in the wind and frighten birds (Figure 3). Structures were once again left for a habituation period of six days and no data were collected until the 7th of February. Phase 2 took place between the 7th and 20th of February 2022.

Measurement of operative temperatures at waterholes

Black bulb thermometers constructed of two 1mm thick copper hemispheres with a diameter of 30mm, superglued together and spray-painted matt black (Bakken *et al.,* 1985; Orolowitz, 2020) and containing iButton dataloggers (Maxim Thermachron iButton™, model DS1922L, Fairbridge Technologies, Sandton, South Africa), were used to measure operative temperature. These were anchored on the front left-hand leg of each structure and weighted down with rocks of the same sediment and size at all waterholes to keep any thermal effects of different substrates constant. They were placed so that the black bulb was underneath the structure 1cm above the ground, hence logging operative temperature conditions similar to those experienced by birds using the shade structure (Figure 4). A stake and length of pine batten was also erected on an open stretch of bank away from the structure to mimic the leg of a structure (in an effort to keep micro climatic conditions constant) and a second black bulb was secured in the same way, the same distance from the water's edge in full sun (Figure 4 & 5). All iButtons were programmed to record a temperature every 10 minutes for the full duration of both phases of the experiment.

Figure 3: Images of structure design and placement in Phase 1 at all sites and at control waterholes in Phase 2 (top row); and at experimental waterholes in Phase 2 (bottom row). Image on the bottom left was taken in the late morning, before shade reached the waters edge at midday.

Figure 4: Image of open bank stake and pine batten used to mimic structure leg onto which camera traps and black bulbs containing iButtons were anchored. Rocks of the same sediment and size were used for weighing down all black bulbs.

Camera placement and bird visitation rate data collection

Two Spartan SR2-BK black flash camera traps were set up at each waterhole to capture bird visitations, and set to take one photograph per minute (see Figure 5). One camera was located on the back right-hand structure leg to capture birds accessing water along the 1.25m stretch of bank shaded/potentially shaded by the structure. Placement was optimized to capture all birds on the ground making use of the structure near/at the water's edge. The second camera was set up on the 'open bank' black bulb stake (Figure 4 and 5). A stretch of open bank at the water's edge equivalent to that shaded by the structure (1.25m) was then demarcated using stones of the same size, spray-painted black, at all of the waterholes (Figure 5). The second camera trap captured bird visitation to this demarcated stretch of the water's edge and was analyzed as the 'open bank' data. The inclusion of a camera monitoring a section of open bank in addition to the one monitoring the area under the shade structure, allowed each waterhole to act as its own control, further strengthening my confidence in the observed interactions being a result of the provision of shade. The open bank cameras also gave an idea of how different species might use a waterhole which is partially-artificially shaded and therefore it allowed me to make inferences on how different species were impacted at a more site-specific scale.

Each waterhole was checked every second day to ensure cameras were functioning correctly, batteries were fully charged and to download the SD cards. The time of day when these checks were conducted was rotated each day for each waterhole to limit disturbance and any effects on birds' daily visitation patterns. The time spent at each waterhole was limited for the same reason.

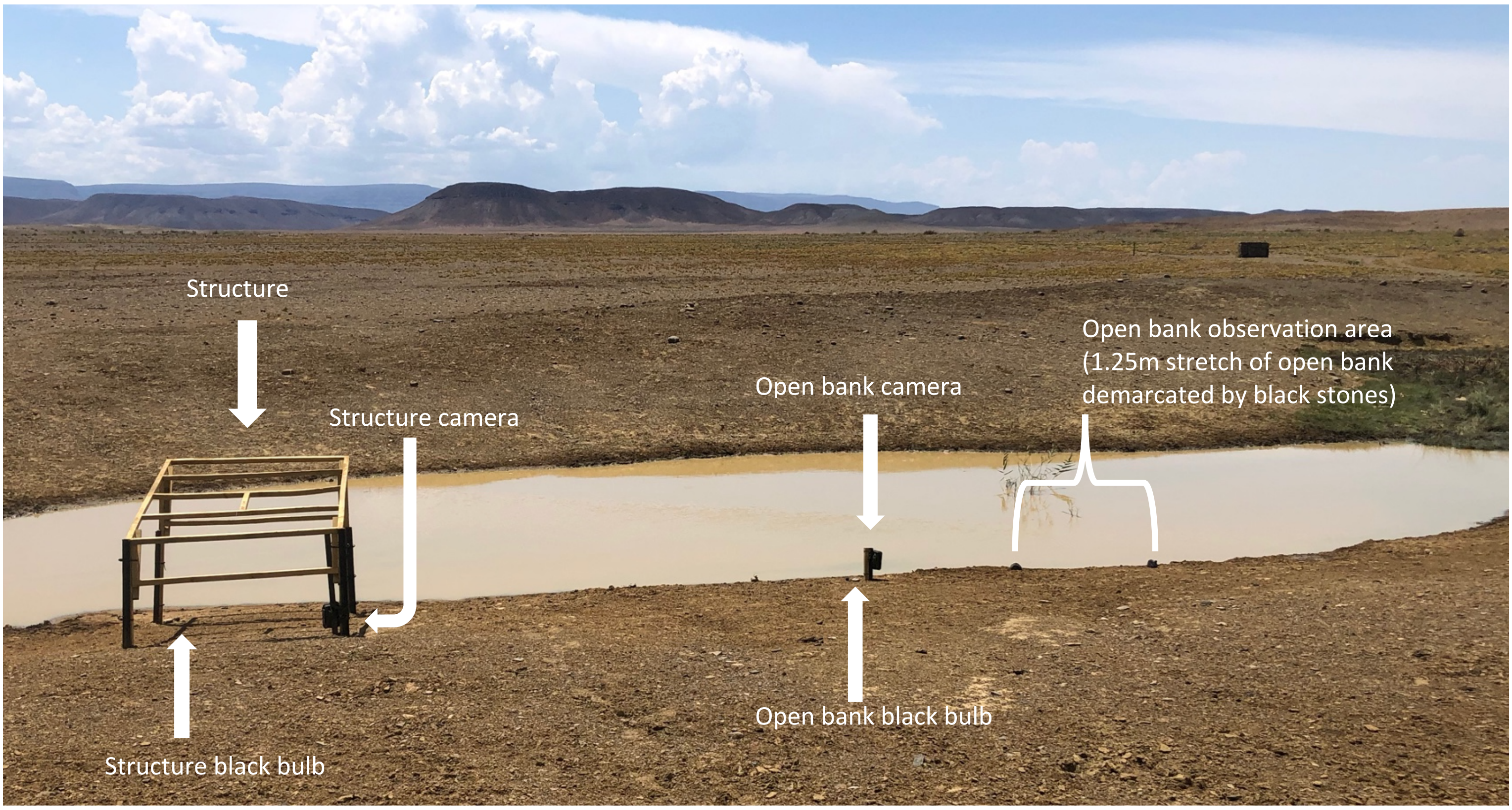


Figure 5: Pramberg North waterhole during Phase 1 showing the annotated experimental design which was replicated at each waterhole.

Statistical analysis

Data extraction

In each phase, data spanning five days were selected for extraction and analysis from each camera (structure and open bank) at each waterhole. These fell between the 20th -29th of January for Phase 1 and between the 10th and the 19th of February for Phase 2. Sunny days with warmer air temperature were prioritized in keeping with my aim of understanding whether providing shade at waterholes can buffer impacts of high temperature by increasing accessibility of water to birds. Due to weather events (such as precipitation and dust storms) and interference with cameras by animals, days were selected on a camera-by-camera basis. Special effort was made to use the same days for structure and open bank data extraction at each waterhole, however this was not always possible. An effort was also made to use the same days at paired waterholes where possible. Black bulb iButton data were analyzed for the same five days per camera, per waterhole, per phase to match the analysis of visitation rates and species richness.

Camera trap photos and temperature data were then divided into five observation blocks; 06:00 - 07:30, 09:00 – 10:30, 12:00 – 13:30, 14:30 – 16:00 and 17:30 – 19:00 during which data were extracted. This was done to ensure an even spread of data collection over the whole day. The first- and second-time blocks (06:00 – 07:30, and 09:00 – 10:30) were combined into the morning or ‘am’ period, while the last three (12:00 – 13:30, 14:30 – 16:00 and 17:30 – 19:00) were combined into the ‘pm’ or afternoon period. The difference in duration between the am and pm periods was not important because I was only interested in the interaction between phase and treatment on the response variables and as such the two time periods were not directly compared. All data handling and analyses were conducted in Microsoft Excel (version 16.62, 2019) and R version 4.0.5 (R Development Core Team, 2019) Using the interface R studio (Rstudio Team, 2016). Models were run in the 'lme4' (*Bates et al.,* 2015) package and 'MASS' (Venables & Ripley, 2002), 'emmeans' (Lenth, 2021), 'RVAideMemoire' (Hervé,2022), 'tidyverse' (Wickham *et al*. 2019) and 'effects' (Fox, 2003) were also used for analyses and creating figures. All maps were made using ArcGIS software (ESRI2011).

Weather data

Long term weather data were sourced from the South African Weather Service (SAWS) for the Calvinia weather station (31.47 °S, 19.78 °E) located ~100km NW of the study site. Data were acquired for a period of 35 years between 1986-2021 and have been used as a proxy for local long term temperature trends. The annual trend of mean maximum daily temperature was analysed for from 1987-2021 using a linear regression across years (le Roux and McGeoch, 2008; Van Wilgen *et al.,* 2016).

Air temperature and rain data from the Roodewerf weather station were analyzed for the full period of each phase. Mean daytime (06:00-19:00) air temperatures and mean daily maximum temperatures were compared between phases using a two-tailed t-test. Mean air temperatures per observation block (06:00 - 07:30, 09:00 – 10:30, 12:00 – 13:30, 14:30 – 16:00 and 17:30 – 19:00) were also calculated using data from the full period of 10 days for each phase. Means per time block were compared using an ANOVA in R. The difference in mean temperature between the morning (06:00-07:30, 09:00-10:30 time blocks combined) and afternoon (12:00 – 13:30, 14:30 – 16:00 and 17:30 – 19:00 time blocks combined) were compared using a two-tailed t-test.

Black bulb data

Linear mixed effect models with Gaussian error distribution were used to analyze the effect of artificial shade on operative temperatures as recorded by open bank and structure black bulbs in the morning and in the afternoon. Fixed effects included in all models were: treatment (control or experimental), phase (Phase 1 before shade and Phase 2 after shade was added at experimental waterholes) and the interaction between phase and treatment. Waterhole and date were included as random effects. Residuals were checked to ensure they followed a normal distribution.

Visitation rates and species-specific models

In each camera trap photo, all birds within the demarcated stretch of water's edge at the structure and open bank were counted and identified to species level. Only birds at or near the water's edge (within 1m) between demarcation markers were counted to increase probability that birds were actually using the water. Because individuals could not be identified, I used "visitation rate" as an index of 'intensity of use' of the waterholes by counting each bird in each photograph for each species and treating each photograph as a new/separate observation.

'Overall' visitation rates were analyzed as a sum of all birds for all species present at the water's edge, in all photos taken per day at both the structure and open bank cameras. Morning and afternoon visitation rates at either the structure or open bank camera were then analysed separately. For the nine most common species (those with > 300 overall records), daily (morning and afternoon combined) visitation rates at the structure and open bank cameras as well as 'overall' (structure and open bank combined) were analysed. Daily visitation rates, rather than hourly visitation rates, were used for the visitation rate analyses due to the low bird density, causing zero-inflation and resulting in convergence issues in the models.

Overall bird visitation rates (all species combined) at structures and open bank cameras were analysed using generalized linear mixed effect models (GLMMs) fitted with a negative binomial distribution. This was done for the morning and afternoon, as well as overall (both cameras and morning and afternoon periods combined). Species-specific visitation rates at structure, open bank and overall (both cameras combined) were analysed using GLMMs fitted with either negative binomial or Poisson distributions as appropriate to the data. For species-specific models, the morning and afternoon periods were combined to avoid zero-inflation. Fixed effects included in all models were: treatment (control or experimental), phase (Phase 1 before shade and Phase 2 after shade was added at experimental waterholes) and the interaction between treatment and phase. Waterhole and date were included as random effects. Over-dispersion was checked in the models by comparing the residual variance and residual degrees of freedom. If a model was over-dispersed an observation level random effect was assigned to each observation by assigning a unique number to each observation row, and then including that column as an additional random effect. This was found to be successful in reducing bias in the parameter estimates and/or standard errors, and successfully addressed overdispersion (Hilbe, 2011; Harrison, 2014; Abdu *et al.,* 2018a). This model structure was applicable to all models in this study and observation level random effects were only assigned where appropriate. Figures for visitation rates are presented to best show the change in visitation across phases While taking background effects into account. Because of this, y-axes are presented as a log scale, however the scales were adapted to present the slopes (and not absolute values) in a legible way. Axes intercept at zero.

Species richness

A total of 29 species were recorded by the camera traps during the course of this study. Species richness was calculated as the total number of species captured by the structure or open bank camera per day as well as overall (combining the structure and open bank cameras) per waterhole in Phase 1 and Phase 2. The interaction between treatment and phase on species richness was analyzed using GLMMs fitted with Poisson error distributions.

Species composition of birds visiting

Visitation rates per hour for the morning and afternoon (structure and open bank and structure cameras combined) for the full duration of the study (Phase 1 and Phase 2 combined) were calculated to investigate the daily timing of drinking by the species recorded in this study. These hourly visitation rates are not related to the daily visitation rates used in the above models. Hourly visitation rates were calculated by dividing the total number of visits in either the morning or afternoon for each species by the number of days in the study

(20 days were analysed, 10 in Phase 1 and 10 in Phase 2) and then dividing the morning visitation rates by 3 (3 hours made up by the two observation blocks in the morning, 06:00-07:30 and 09:00-10:30) and by 4.5 in the afternoon (4.5 hours in the afternoon made up by the 3 observation blocks in the afternoon, 12:00-13:30, 14:30-16:00, 17:30-19:00).

Changes in the timing of bird visits in response to shade structures

GLMMs fitted with binomial distributions were used to assess whether there was a shift in the timing of the majority of bird visits from morning to afternoon as a result of the addition of artificial shade. This was done by analysing the interaction between treatment and phase on the proportion of visits in the afternoon versus the morning at (1) structures (2) open bank and (3) overall (both cameras summed).

Results

Air temperature and precipitation events from the Roodewerf weather station

Daytime air temperature (06:00-19:00) during the study period ranged from 18.7°C to 41.4°C (Figure 6). Mean daytime air temperatures were significantly higher (t = 9.03, df = 269, P = <0.01) in Phase 1 before shade was added at experimental waterholes (mean and standard deviation: 33.21 ± 4.51°C) than in Phase 2 after shade was added at experimental waterholes (30.73 ± 4.20°C). Mean maximum daily air temperatures (Phase 1 = 38.05 ± 2.34 °C, Phase 2 = 34.83 ± 2.70) were also significantly higher in the first phase (t = 2.995, df = 20, P = 0.004). The maximum daytime air temperatures recorded during the study were 41.4°C in Phase 1 and 38.4°C in Phase 2. Two precipitation events occurred in Phase 1 with a total of 5.3 mm of rainfall, while one precipitation event of 0.5 mm occurred in Phase 2 (Figure 6).

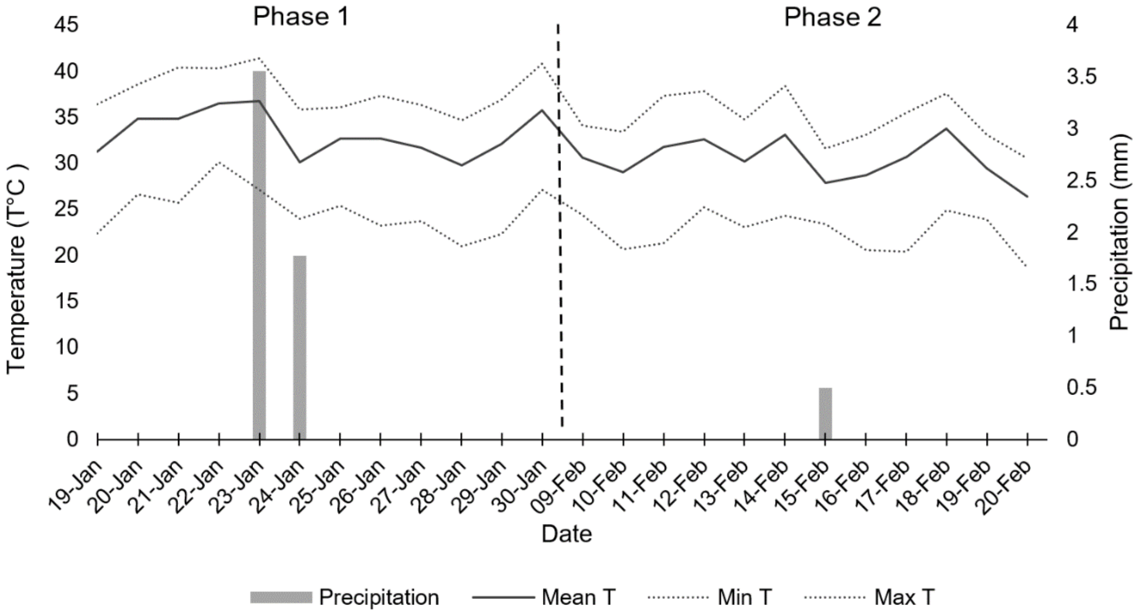


Figure 6: Mean (±SE), maximum and minimum air temperature (T), as well as precipitation over the study period measured at the Roodewerf reception weather station in the Tankwa Karoo National Park. Data were analysed from the 20th- 29th of January 2022 (Phase 1) and from the 10th-19th of February 2022 (Phase 2).

Air temperatures over the entire study period (Phase 1 and 2) increased throughout the day, peaking in the third (12:00-13:30) and fourth (14:30-16:00) observation blocks (Figure 7). Mean air temperatures remained high during the fifth observation block (17:30-1900, Figure 2). These three time blocks made up the ‘afternoon/pm’ study period and had a mean temperature of 32.87 ± 2.37°C. Time block one (06:00-07:30) and block two (09:00-10:30) made up the ‘morning/am’ study period and had a mean temperature of 28.14 ± 3.59°C. Mean air temperatures were significantly higher in the afternoon (t = 11.92, df = 340.73, P<0.01) than the morning.

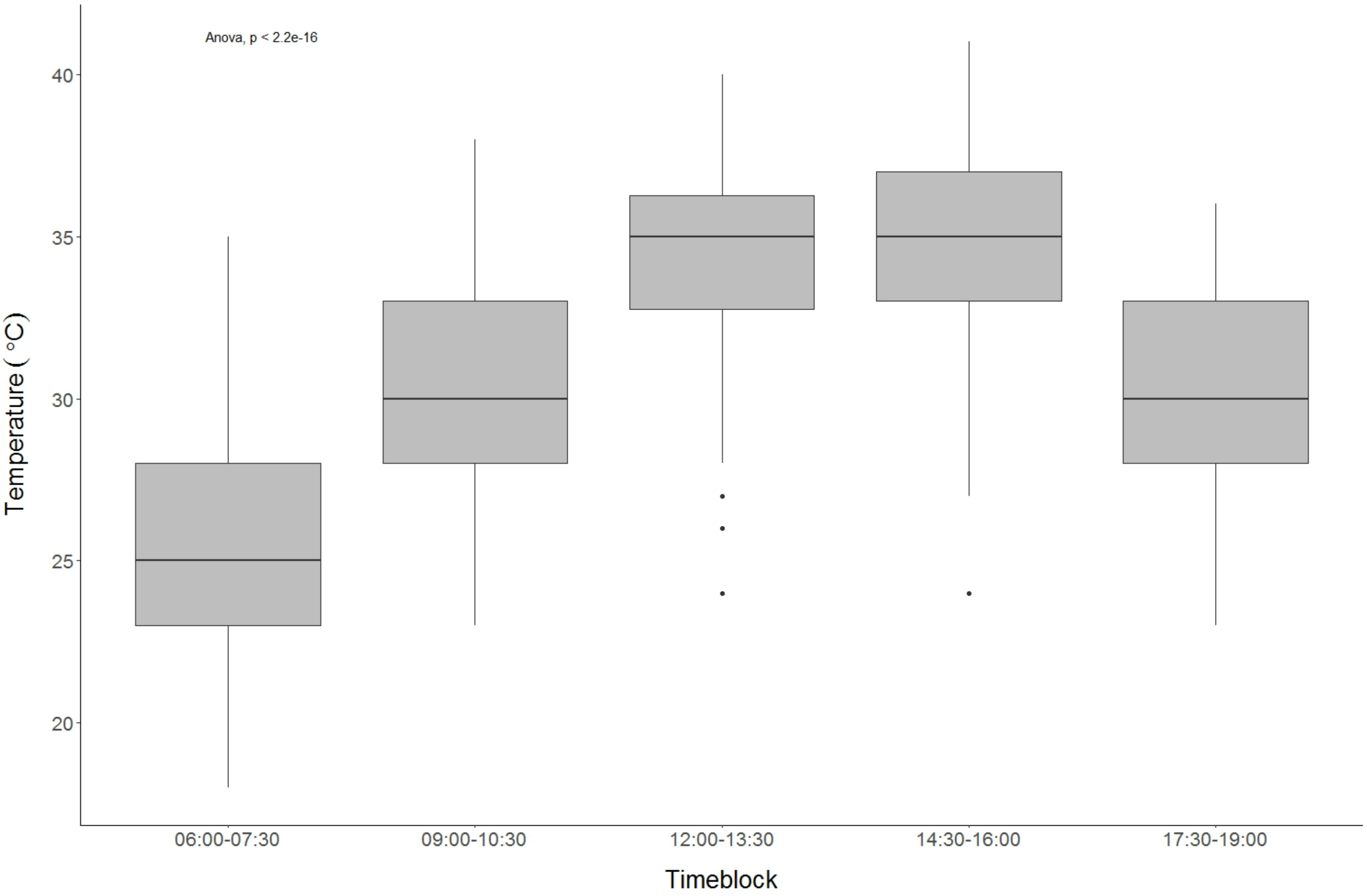
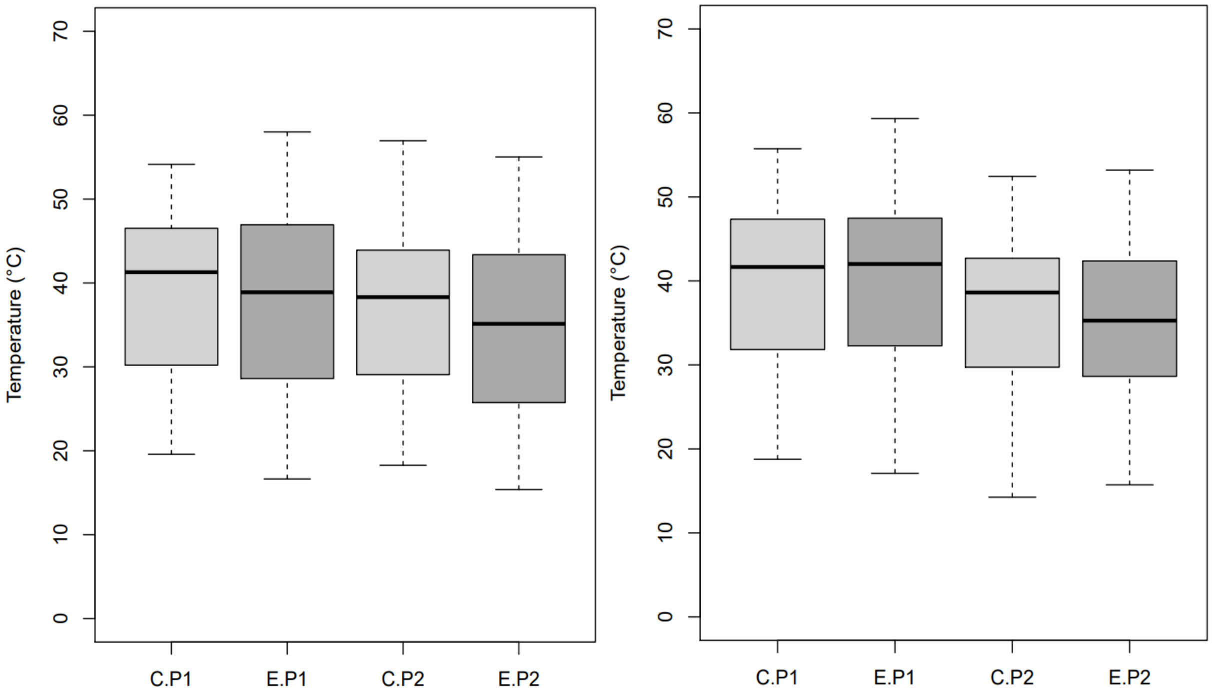


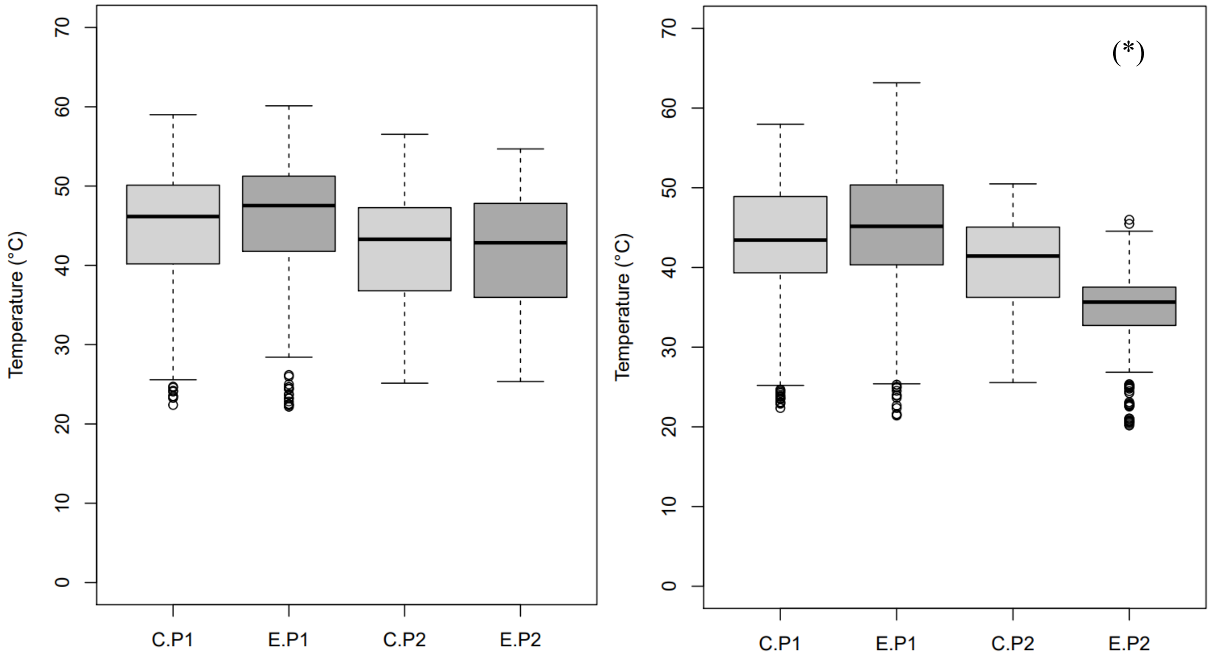
Figure 7: Daytime air temperature patterns for the five time blocks from which data were extracted in this study. Boxplots show the median temperature (central line), inter-quartile range (box edges), temperature range (whiskers) and outliers (black dots) for daily mean air temperature per observation block over the full study period (Phase 1 and Phase 2 combined).

Black bulb temperatures

Black bulb temperatures during the observation time blocks ranged from 14.3°C in the early morning at the Stonefence waterhole (open bank) in Phase 2, to 63.2°C in the afternoon at the Abrahamsknee waterhole (structure) in Phase 1. No significant interaction was found between treatment (experimental where shade was added vs control) and experimental phase (Phase 1: before shade and Phase 2: after shade) on black bulb temperature for open bank black bulbs in the morning; structure black bulbs in the morning; or open bank black bulbs in the afternoon (Table 1, Figure 8). A significant interaction was seen between treatment and experimental phase in black bulb temperature at structure sites in the afternoon (est. -7.13, SE = 0.60, $P<0.01$; see Table 1 for full model outputs). Black bulb temperatures were more than 9°C lower under shaded structures (experimental) in the afternoon (mean and standard deviation: 32.1 ± 5.3°C) relative to unshaded (control) structures (41.9 ± 5.8°C).



A. Morning Open bank B. Morning Structure



C. Afternoon Open bank D. Afternoon Structure

Figure 8: Black bulb temperatures in the morning and afternoon on open bank and under the structure. A significant drop in temperature under the structure after shade was added at experimental waterholes can be seen in panel D, significance ($P<0.05$) shown with a (*). The morning period comprises the mean temperatures of the 06:00-07:30 and 09:00-10:30 observation blocks while the afternoon period comprises mean temperatures for the 12:00-13:30, 14:30-16:00 and 17:30-19:00 time blocks. Boxplots show the median temperature (central line), inter-quartile range (box edges), temperature range (whiskers) and outliers (open circles) of control (light grey) and experimental (dark grey) waterholes (including 3 control waterholes where no structures were shaded and 3 experimental waterholes where shade was provided) in Phase 1 (pre-shading) and Phase 2 (shaded). C= control, E= experimental, P1= Phase 1, P2= Phase 2.

Table 1: Table 1: Model outputs for the interaction between treatment (control waterholes where no shade was added to structures, vs experimental where shade was added) and experimental phase (Phase 1: before shade was added, and Phase 2: after shade was added) on the temperature recorded by iButtons within black bulbs in the morning and afternoon located under structures or on open bank. Models were linear mixed models fitted with a gaussian distribution and waterhole and date were included as fixed effects. Phase 1 and Treatment: control are set as baselines. Bold type indicates significant effects.

Morning

Response variable	Factor	Estimate	SE	t-value	P-value
Open bank black bulb temperature °C	***Intercept***	***34.50***	***2.06***	***16.72***	**<0.01**
	Phase (Phase 2)	-1.08	1.28	-0.85	0.41
	Treatment (Experimental)	-1.74	2.71	-0.64	0.55
	Treatment*Phase	-1.42	1.06	-1.35	0.18
Structure black bulb temperature °C	***Intercept***	***35.53***	***1.77***	***20.08***	**<0.01**
	Phase (Phase 2)	-2.64	1.45	-1.82	0.08
	Treatment (Experimental)	-0.50	2.15	-0.23	0.83
	Treatment*Phase	-0.24	1.09	-0.22	0.82

Afternoon

Response variable	Factor	Estimate	SE	t-value	P-value
Open bank black bulb temperature °C	***Intercept***	***45.03***	***1.29***	***34.88***	**<0.01**
	Phase (Phase 2)	**-3.14**	**1.47**	**-2.14**	**0.05**
	Treatment (Experimental)	0.90	1.14	0.79	0.47
	Treatment*Phase	-1.02	0.70	-1.46	0.14
Structure black bulb temperature °C	***Intercept***	***43.45***	***1.65***	***26.38***	**<0.01**
	Phase (Phase 2)	-2.80	1.42	-1.97	0.07
	Treatment (Experimental)	1.21	1.86	0.65	0.55
	Treatment*Phase	**-7.13**	**0.60**	**-11.83**	**<0.01**

Bird visitation rates to waterholes

A total of 9,025 waterhole visits by 29 bird species were recorded during this study. Bird visitation was assessed in the mornings and afternoons at structure and open bank cameras for all species combined over a 10-day period (five days in Phase 1, and five days in Phase 2).

At structure cameras in the afternoon, a significant positive interaction on bird visitation rates was found between treatment (experimental shade added vs control) and experiment phase (Phase 1: before shade and Phase 2: after shade was added) (Figure 9) where there was an increase in bird visitation to shaded structures and a decline in visitation at control (unshaded) structures (est. 1.54, SE = 0.43, P < 0.01, Table 2, Figure 9). In contrast, a significant negative interaction was found at structures in the morning (Figure 9) where there was a decrease in bird visitation in Phase 2 to shaded structures and an increase in visitation to unshaded structures at control waterholes (est. -2.25, SE = 0.44, $P < 0.01$, Table 2, Figure 9).

There was no significant interaction between phase and treatment on bird visitation rates at the open bank cameras in the morning or in the afternoon (Figure 9 & Table 2). No significant interaction was found between phase and treatment on overall bird visitation rates (full days at structure and open bank cameras combined) (Figure 9, see Table 2 for full model outputs).

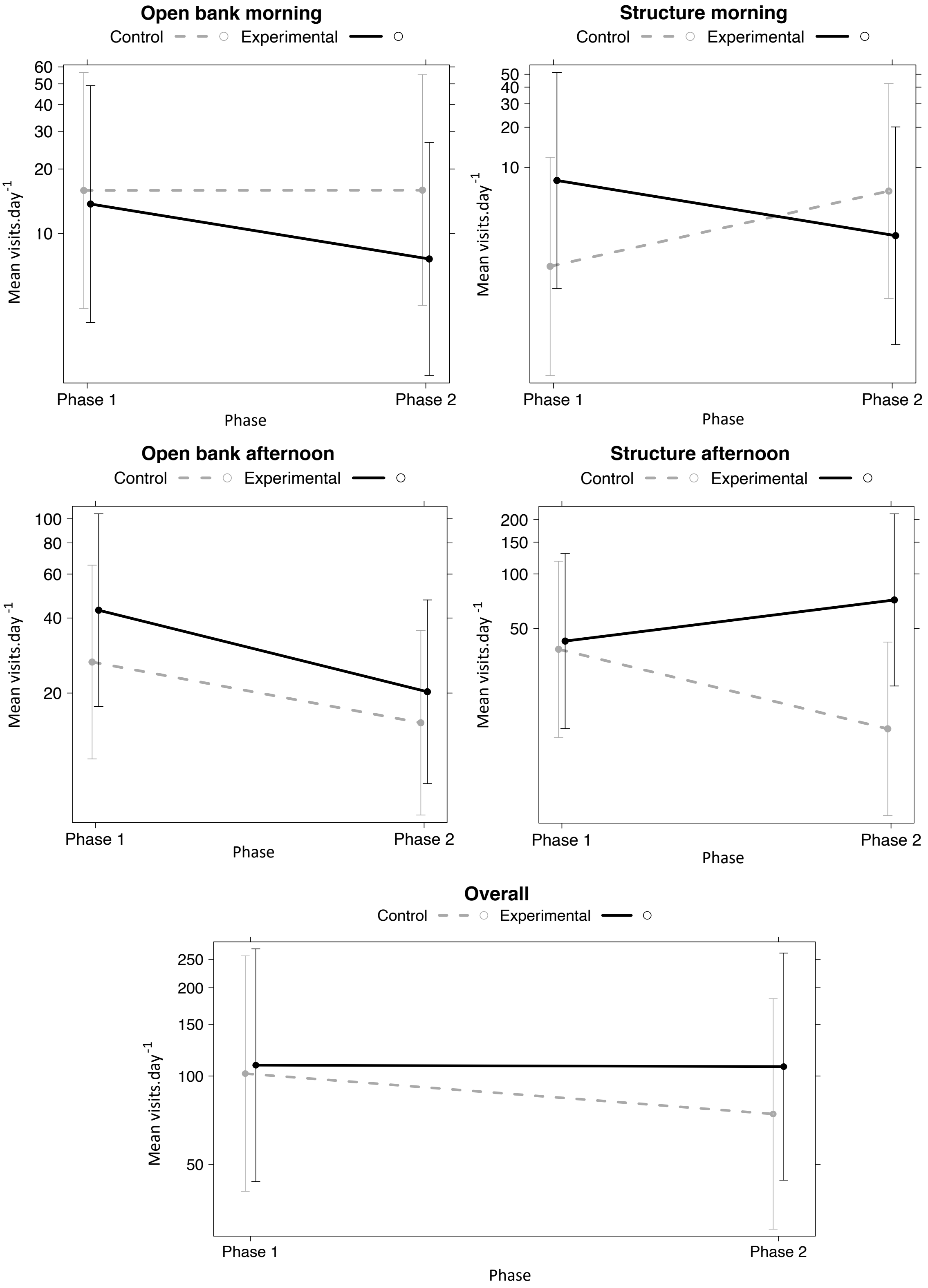


Figure 9: Daily bird visitation rates in the morning (P < 0.01) and afternoon (P < 0.01) at structures, on open bank and overall (structure and open bank cameras combined, P = 0.43). The morning period is the visitation rate (mean visits per day) in the 06:00-07:30 and 09:00-10:30 observation blocks while the afternoon period is the visitation rate in the 12:00-13:30, 14:30-16:00 and 17:30-19:00 observation blocks. Control waterholes (grey circles and dotted lines) received no shade while experimental waterholes (black circles and solid line) received shade in Phase 2. Error bars show 95 % confidence intervals for mean visits per day. y-Axis is presented as a logarithmic scale and axes intercept at 0.

Table 2: Model outputs for the interaction between treatment (experimental: where no shade was added, vs control: where shade was added) and experimental phase (Phase 1: before shade was added, and Phase 2: after shade was added) on bird visitation rates (all species combined) in the morning (06:00-07:30, 09:00-10:30) and afternoon (12:00-13:30, 14:30-16:00, 17:30-19:00) under structures or on open bank, as well as overall (open bank and structure cameras combined). Models were GLMMs fitted with a negative binomial distribution. Waterhole and date were included as random effects, Phase 1 and Treatment: control are set as baselines. Bold type indicates significant effects.

Structure

Response variable	Factor	Estimate	SE	Z- Statistic	P-value
Morning bird visitation rate	*Intercept*	*0.59*	*0.94*	*0.63*	*0.53*
	Phase (Phase2)	**1.30**	**0.33**	**3.90**	**<0.01**
	Treatment (Experimental)	1.48	1.32	1.13	0.26
	Treatment*Phase	**-2.25**	**0.44**	**-5.17**	**<0.01**
Afternoon bird visitation rate	***Intercept***	***3.65***	***0.56***	***6.50***	***<0.01***
	Phase (Phase2)	**-1.01**	**0.44**	**-2.32**	**0.02**
	Treatment (Experimental)	0.10	0.72	0.14	0.89
	Treatment*Phase	**1.54**	**0.43**	**3.58**	**<0.01**

Open bank

Response variable	Factor	Estimate	SE	Z- Statistic	P-value
Morning bird visitation rate	*Intercept*	***2.77***	***0.63***	***4.36***	***<0.01***
	Phase (Phase2)	0.00	0.41	0.01	0.99
	Treatment (Experimental)	-0.15	0.84	-0.17	0.86
	Treatment*Phase	-0.60	0.45	-1.33	0.19
Afternoon bird visitation rate	*Intercept*	***3.28***	***0.45***	***7.35***	***<0.01***
	Phase (Phase2)	-0.56	0.42	-1.35	0.18
	Treatment (Experimental)	0.48	0.54	0.88	0.38
	Treatment*Phase	**-0.19**	0.42	-0.46	0.65

Overall

Response variable	Factor	Estimate	SE	Z- Statistic	P-value
Overall bird visitation rate	*Intercept*	***4.63***	***0.46***	***10.02***	***<0.01***
	Phase (Phase2)	-0.32	0.38	-0.83	0.41
	Treatment (Experimental)	0.07	0.59	0.11	0.91
	Treatment*Phase	0.31	0.39	0.79	0.43

Species-specific visitation rates

Of the 29 species recorded in this study, nine were recorded over 300 times and were therefore used for species-specific analyses (Table 3). Different species responded in varying ways to the presence of shaded structures and of the nine most common species, four significantly altered their visitation rates in relation to the addition of shade. These species showed a significant interaction between waterhole treatment group (experimental vs control) and experimental phase (Phase 1 and 2) on visitation rate (Table 3, Figure 10). Grey-backed Sparrow-larks (*Eremopterix verticalis*) and Tractrac Chats (*Emarginata tricrac*) showed a significant positive response while Cape Sparrows (*Passer melanurus*) and White-throated Canaries (*Crithangra albogularis*) showed a significant negative response (Table 3, Figure 10).

Grey-backed Sparrow-lark visitation rates showed a positive interaction between treatment and experimental phase, such that the overall decline in mean visitation rates to all waterholes (structure and open bank cameras combined) between Phase 1 and 2 was buffered at experimental waterholes relative to control waterholes (est. 2.73, SE = 0.73, P < 0.01, Figure 10 & Table 3). This was reflected by a significant positive interaction between treatment and phase at open bank cameras (est. 1.58, SE = 0.76, P = 0.037) but not at structure cameras (although the interaction was near-significant: est. 2.85, SE = 1.51, P = 0.061; see Table 3 for full model outputs).

Tractrac Chat visitation rates showed a positive interaction between treatment and phase, such that there was an overall increase in visitation rates at experimental waterholes relative to a decrease at control waterholes (est. 3.64, SE = 0.46, P < 0.01, Figure 10). A significant positive interaction between treatment and phase was seen at structure cameras (est. 4.56, SE = 0.57, P < 0.01) but there was no significant interaction at open bank cameras.

Cape Sparrow visitation rates showed a negative interaction between treatment and phase, such that an overall increase in mean visitation rates seen at control waterholes between Phase 1 and Phase 2 was suppressed at experimental waterholes (est. -3.49, SE = 0.38, P < 0.01, Figure 10). This was reflected by a negative interaction between treatment and phase at both the open bank cameras (Est: -4.75, SE = 0.50, P < 0.01) and at structure cameras (est. -2.96, SE = 0.79, P < 0.01; see Table 3 for full model outputs).

White-throated Canary visitation rates showed a negative interaction between treatment and phase, such that there was an overall increase in mean visitation rates at control waterholes and a decrease at experimental waterholes (est. -4.01, SE = 0.75, P < 0.01, Figure 10). This was reflected by a negative interaction between treatment and phase at the structure cameras (est. -3.70, SE = 0.83, P < 0.01). The model at the open bank cameras did not converge (see Table 3 for full model outputs).

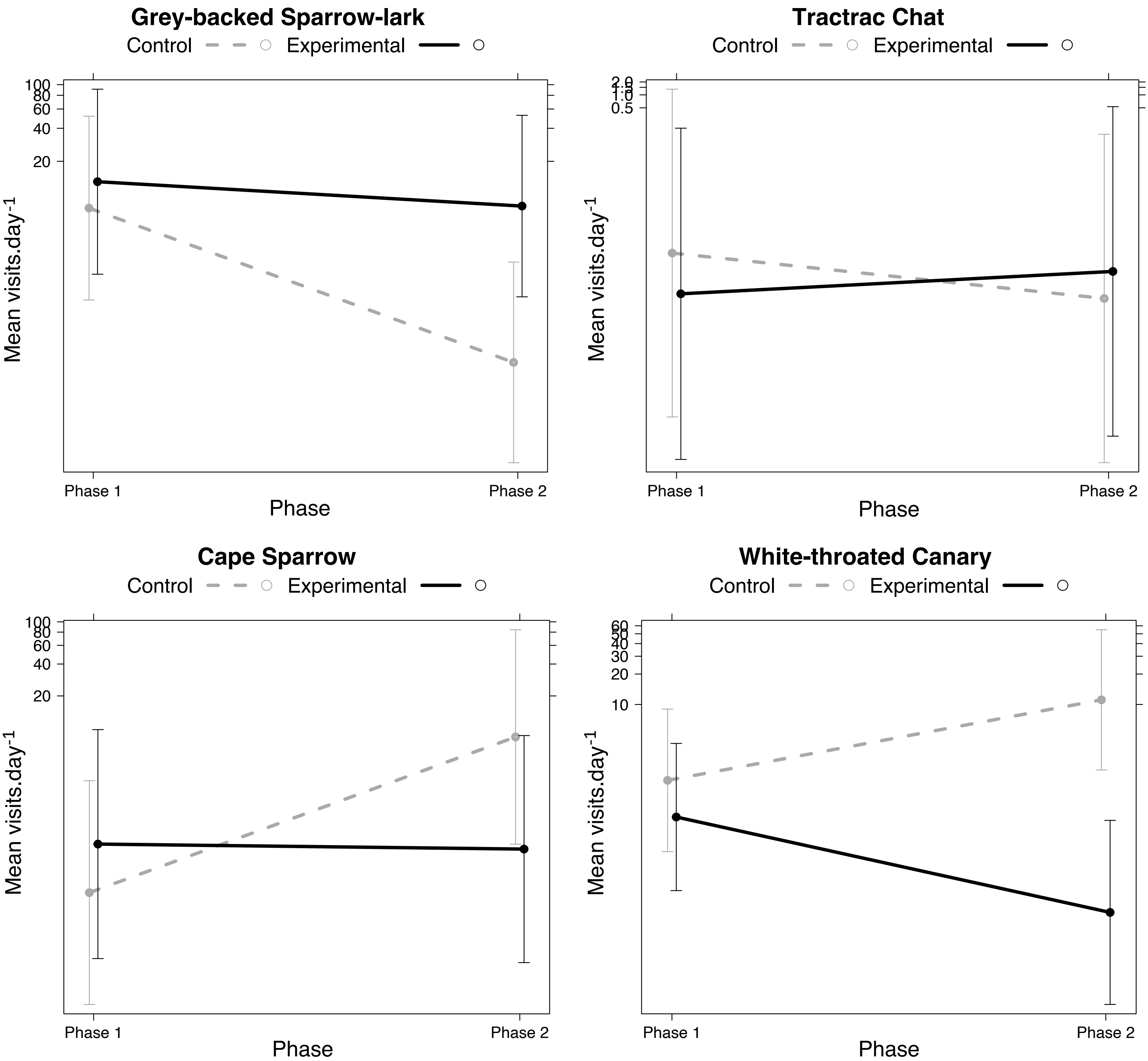


Figure 10: Daily Species-specific overall visitation rate (open bank and structure cameras, and morning and afternoon periods combined) for the two positive responding species (top row, $P < 0.01$)): Grey-backed Sparrow-lark and Tractrac Chat; and two negatively responding species (bottom row, $P < 0.01$): Cape Sparrow and White-throated Canary. Control waterholes (grey circles and dotted lines) received no shade while experimental waterholes (black circles and solid line) received shade in Phase 2. Error bars show 95% confidence intervals for mean visits per day. y-Axis is presented as a logarithmic scale and axes intercept at 0.

Table 3: Model outputs for the interaction between treatment (experimental: where no shade was added, vs control: where shade was added) and experimental phase (Phase 1: before shade was added, and Phase 2: after shade was added) on species (as specified) visitation under structures or on open bank, as well as overall (open bank and structure cameras combined). Visitation rates were calculated as the sum of all individuals of that species seen in the photographs for that day. Models were GLMMs fitted with negative binomial or Poisson distribution (as specified) and waterhole and date included as random effects as well as an observation level random effect where necessary to control for over-dispersion. Treatment: control and Phase 1 are set as baselines. Bold type indicates significant effects.

Response variable	Model fit	Factor	Estimate	SE	Z- Statistic	P-value
Grey-backed Sparrow-larks at structure	Negative binomial	*Intercept*	***1.79***	***0.57***	***3.14***	***<0.01***
		Treatment (Experimental)	**1.98**	**0.80**	**2.47**	**0.01**
		Phase (Phase2)	**-4.50**	**1.28**	**-3.51**	**<0.01**
		Treatment*Phase	2.85	1.52	1.88	0.06
Grey-backed Sparrow-larks at open bank	Negative binomial	*Intercept*	*1.72*	*0.94*	*1.83*	*0.07*
		Treatment (Experimental)	0.64	1.29	0.50	0.62
		Phase (Phase2)	**-2.54**	**0.65**	**-3.91**	**<0.01**
		Treatment*Phase	**1.58**	**0.76**	**2.09**	**0.04**
Grey-backed Sparrow-larks overall	Negative binomial	*Intercept*	***2.01***	***0.96***	***2.09***	***0.04***
		Phase (Phase2)	**-3.24**	**0.91**	**-3.56**	**<0.01**
		Treatment (Experimental)	0.55	1.17	0.48	0.64
		Treatment*Phase	**2.73**	**0.73**	**3.75**	**<0.01**
Red-capped Larks at structure	Negative binomial	Intercept	***3.02***	***0.74***	***4.09***	***<0.01***
		Treatment (Experimental)	1.59	1.09	1.46	0.14
		Phase (Phase2)	**-2.00**	**0.69**	**-2.92**	**0.00**
		Treatment*Phase	1.55	1.13	1.38	0.17
Red-capped Larks at open bank	Negative binomial	*Intercept*	***2.85***	***0.39***	***7.30***	***<0.01***
		Treatment (Experimental)	0.25	0.42	0.58	0.56
		Phase (Phase2)	**-1.15**	**0.46**	**-2.53**	**0.011***
		Treatment*Phase	0.91	0.48	1.89	0.06
Red-capped Larks overall	Poisson	*Intercept*	***3.50***	***0.47***	***7.52***	***<0.01***
		Phase (Phase2)	**-1.46**	**0.52**	**-2.80**	**0.01**
		Treatment (Experimental)	-0.81	0.52	-1.56	0.12
		Treatment*Phase	0.92	0.50	1.87	0.06
Namaqua Sandgrouse at structure	Poisson	*Intercept*	*-2.03*	*1.21*	*-1.69*	*0.09*
		Treatment (Experimental)	2.72	1.79	1.52	0.13
		Phase (Phase2)	0.09	1.09	0.08	0.93
		Treatment*Phase	2.19	1.40	1.56	0.12
Namaqua Sandgrouse at open bank	Poisson	*Intercept*	*0.83*	*1.25*	*0.67*	*0.51*
		Treatment (Experimental)	0.76	1.62	0.47	0.64

		Phase (Phase2)	**-1.50**	**0.61**	**-2.45**	**0.01**
		Treatment*Phase	-0.36	0.25	-1.42	0.16
Namaqua Sandgrouse overall	Negative binomial	*Intercept*	***1.77***	***0.73***	***2.41***	***0.02***
		Phase (Phase2)	-0.93	0.58	-1.61	0.11
		Treatment (Experimental)	0.23	1.03	0.23	0.82
		Treatment*Phase	-0.59	0.79	-0.75	0.45
White-necked Raven at structure	Poisson	*Intercept*	*-24.43*	*62.93*	*-0.39*	*0.70*
		Treatment (Experimental)	21.28	62.93	0.34	0.74
		Phase (Phase2)	-1.14	70.73	-0.02	0.99
		Treatment*Phase	1.62	70.74	0.02	0.98
White-necked Raven at open bank	Did not converge			Did not converge		
White-necked Raven overall	Negative binomial (singular fit)	*Intercept*	*-35.93*	*185.42*	*-0.19*	*0.85*
		Phase (Phase2)	0.60	136.23	0.00	1.00
		Treatment (Experimental)	35.33	185.42	0.19	0.85
		Treatment*Phase	-0.38	136.24	0.00	1.00
Cape Sparrow at structure	Poisson	*Intercept*	*-2.43*	*1.47*	*-1.65*	*0.10*
		Treatment (Experimental)	1.25	2.02	0.62	0.54
		Phase (Phase2)	**2.75**	**0.89**	**3.08**	**0.00**
		Treatment*Phase	**-2.96**	**0.79**	**-3.73**	**<0.01**
Cape Sparrow at open bank	Poisson	*Intercept*	***-2.12***	***1.04***	***-2.05***	***0.04***
		Treatment (Experimental)	1.47	1.35	1.08	0.28
		Phase (Phase2)	**3.84**	**0.63**	**6.12**	**<0.01**
		Treatment*Phase	**-4.75**	**0.50**	**-9.55**	**<0.01**
Cape Sparrow overall	Poisson	*Intercept*	*-1.28*	*1.24*	*-1.03*	*0.30*
		Phase (Phase2)	**3.38**	**0.54**	**6.31**	**<0.01**
		Treatment (Experimental)	1.06	1.72	0.61	0.54
		Treatment*Phase	**-3.49**	**0.38**	**-9.27**	**<0.01**
Lark-like Bunting at structure	Poisson	*Intercept*	*-1.26*	*2.10*	*-0.60*	*0.55*
		Treatment (Experimental)	0.37	2.89	0.13	0.90
		Phase (Phase2)	-0.63	0.51	-1.23	0.22
		Treatment*Phase	-0.85	0.44	-1.94	0.05
Lark-like Bunting at open bank	Poisson	*Intercept*	*-1.91*	*1.90*	*-1.01*	*0.32*
		Treatment (Experimental)	0.76	2.55	0.30	0.77
		Phase (Phase2)	**-1.53**	**0.78**	**-1.96**	**0.05**
		Treatment*Phase	1.08	0.65	1.66	0.10
Lark-like Bunting overall	Poisson	*Intercept*	*-0.61*	*1.72*	*-0.36*	*0.72*
		Phase (Phase2)	**-1.06**	0.49	**-2.18**	**0.03**

		Treatment (Experimental)	0.75	2.37	0.32	0.75
		Treatment*Phase	-0.01	0.35	-0.04	0.97
White-throated Canary at structure	Poisson	*Intercept*	*-0.96*	*1.53*	*-0.63*	*0.53*
		Treatment (Experimental)	0.69	2.12	-0.33	0.75
		Phase (Phase2)	**2.03**	**0.34**	**5.90**	**<0.01**
		Treatment*Phase	**-3.70**	**0.83**	**-4.45**	**<0.01**
White-throated Canary at open bank	Did not converge	Did not converge				
White-throated Canary overall	Poisson	*Intercept*	*0.57*	*0.83*	*0.69*	*0.49*
		Phase (Phase2)	**1.83**	**0,25**	**7.22**	**<0.01**
		Treatment (Experimental)	-0.83	1.17	-0.71	0.48
		Treatment*Phase	**-4.01**	**0.75**	**-5.38**	**<0.01**
Tractrac Chat at structure	Poisson	*Intercept*	*-8.77*	*4.49*	*-1.95*	*0.05*
		Treatment (Experimental)	-2.92	4.95	-0.59	0.56
		Phase (Phase2)	-1.99	1.33	-1.50	0.14
		Treatment*Phase	**4.56**	**0.57**	**8.02**	**<0.01**
Tractrac Chat at open bank	Poisson	*Intercept*	*-7.13*	*5.05*	*-1.41*	*0.16*
		Treatment (Experimental)	0.35	4.26	0.08	0.93
		Phase (Phase2)	-0.48	0.88	-0.54	0.59
		Treatment*Phase	-0.86	1.26	-0.69	0.49
Tractrac Chat overall	Poisson	*Intercept*	*-8.49*	*4.49*	*-1.89*	*0.06*
		Phase (Phase2)	**-2.44**	**1.12**	**-2.17**	**0.03**
		Treatment (Experimental)	-2.19	4.98	-0.44	0.66
		Treatment*Phase	**3.64**	**0.46**	**7.85**	**<0.01**

The four responding species i.e., Grey-backed Sparrow-larks, Tractrac Chats, White-throated Canaries and Cape Sparrows made up 26.5%, 3.5%, 6.0% and 6.3% of birds recorded in the study respectively. Of the positive responders, the majority of Grey-backed Sparrow-larks (77.5%) were observed at the Abrahamsknee waterhole, while 100% of the Tractrac Chats were observed at the Varschfontein and Stonefence waterholes. Of the negative responders, 72.4% of White-throated Canaries were observed at the Perdekop waterhole, while 57.8% of Cape Sparrows were observed at the Varschfontein waterhole.

Species richness

No significant effects of treatment, phase, or their interaction on species richness were found at structure cameras, open bank cameras, or overall (all P > 0.05, Table 4).

Table 4: Model outputs for the interaction between treatment (experimental: where no shade was added, vs control: where shade was added) and experimental phase (Phase 1: before shade was added, and Phase 2: after shade was added) on species richness under structures or on open bank, as well as overall (open bank and structure cameras combined). Models were GLMMs fitted with Poisson distribution and waterhole and date included as random effects, Treatment: control and Phase 1 are set as baselines. Bold type indicates significant effects.

response variable	Model fit	Factor	Estimate	SE	Z-statistic	P-value
Species richness at structure	Poisson	*Intercept*	***1.30***	***0.20***	***6.62***	***<0.01***
		Treatment (Experimental)	0.20	0.27	0.77	0.44
		Phase (Phase2)	-0.26	0.21	-1.26	0.21
		Treatment*Phase	-0.01	0.27	-0.05	0.96
Species richness at open bank	Poisson	*Intercept*	***1.64***	***0.21***	***7.71***	***<0.01***
		Treatment (Experimental)	0.11	0.28	0.40	0.69
		Phase (Phase2)	-0.06	0.19	-0.35	0.73
		Treatment*Phase	-0.37	0.23	-1.60	0.11
Species richness overall	Poisson	*Intercept*	***1.88***	***0.18***	***10.33***	***<0.01***
		Treatment (Experimental)	-0.20	0.17	-1.18	0.24
		Phase (Phase2)	0.08	0.24	0.31	0.76
		Treatment*Phase	-0.27	0.21	-1.29	0.20

Species composition of birds visiting

Although species richness did not change across the course of the experiment, the proportion of total visits by different species to waterholes, and by extension, water use by the bird community differed overall (combining structure and open bank cameras) between Phase 1 and Phase 2 (Figure 11). In Phase 1, Grey-backed Sparrow-larks (39.2%) and Red-capped Larks (30.1%) made up the bulk of visits, followed by Lark-like Buntings (13.1%) and Namaqua Sandgrouse (6.0%). In comparison these same species only accounted for 12.3%, 15.2%, 6.2% and 3.4% respectively in Phase 2. There was an overall decline in the bird visitations between the two phases (44.3% drop in bird visitation of the nine most common species) which led to an increase in the proportion of visitation by species other than the four listed above in Phase 2.

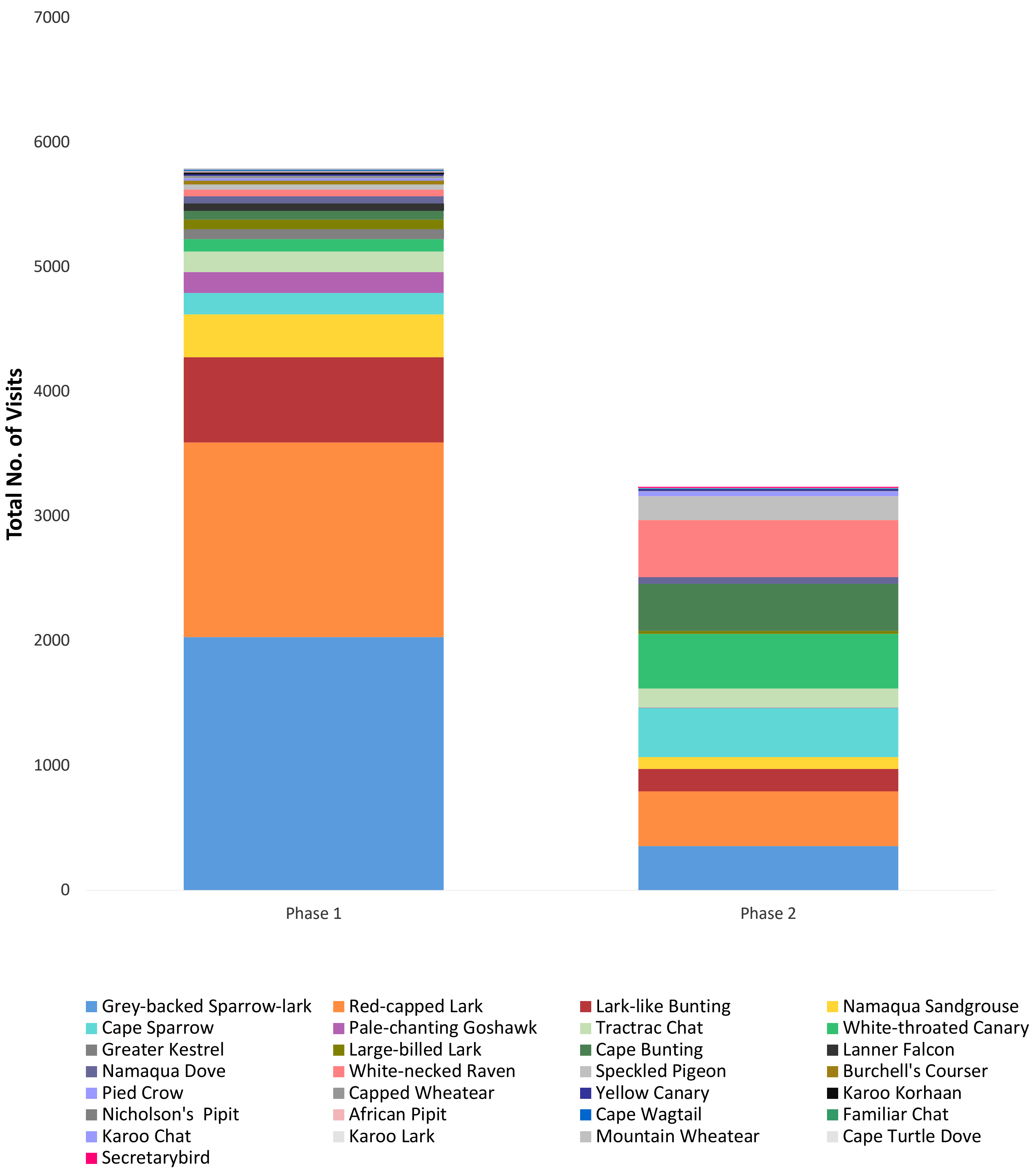


Figure 11: Species composition and the relative total number of visits by species (all waterholes and structure and open bank cameras combined) in Phase 1 (before the addition of artificial shade) and Phase 2 (after the addition of artificial shade at experimental waterholes), showing an overall decline in the total number of bird visits in Phase 2 and change in relative numbers of the different species.

Of the species recorded in this study, 15 accessed water more frequently in the afternoon, shown by their higher overall visitation rate per hour in the afternoon for the duration of this study (Table 5). Nine species accessed water more frequently in the morning and the remainder appeared to access water equally or near equally in the morning and afternoon (Table 5). Of the four responding species, Grey-backed Sparrow-larks and Tractrac Chats accessed water more frequently in the afternoon while Cape Sparrows had a similar visitation rate per hour in both the morning and afternoon (Table 5). White-throated Canaries accessed waterholes more frequently in the morning during the full study period (Table 5).

Table 5: The 29 species recorded in this study, their typical body mass (g) and the total number of visits to waterholes (all cameras combined for both phases) by each species during the study period. Mean visitation rates per hour for the morning and afternoon are also provided for each species. Bold type shows the nine most common species (>300 visits).

Species	Mass (g)	Overall visits	AM visitation rate per hour	PM visitation rate per hour
Grey-backed Sparrow-lark (*Eremopterix verticalis*)	**17**	**2387**	8.18	21.07
Red-capped Lark (*Calandrella cinerea*)	**24**	**2001**	4.62	19.16
Lark-like Bunting (*Emberiza impetuani*)	**15**	**860**	7.45	4.59
Cape Sparrow (*Passer melanurus*)	**26**	**564**	3.42	3.99
White-throated Canary (*Crithangra albogularis*)	**27**	**539**	6	1.99
White-Necked Raven (*Corvus albicollis*)	**800**	**512**	0.4	5.42
Cape Bunting (*Emberiza capensis*)	**20**	**449**	2.5	3.32
Namaqua Sandgrouse (*Pterocles namaqua*)	**180**	**444**	3.13	2.84
Tractrac Chat (*Emarginata tractrac*)	**24**	**313**	0.05	3.44
Speckled Pigeon (*Columba guinea*)	345	232	0	2.57
Pale-chanting Goshawk (*Melierax canotus*)	495-1250	175	0.08	1.89
Namaqua Dove (*Oena capensis*)	40	112	0.1	1.18
Large-billed Lark (*Galerida magnirostris*)	45	100	0.45	0.81
Greater Kestrel (*Falco rupicoloides*)	250-265	79	0.1	0.81
Lanner Falcon (*Falco biarmicus*)	725	60	0.32	0.46
Pied Crow (*Corvus albus*)	550	58	0.43	0.36
Burchell's Courser (*Cursorius rufus*)	88	30	0.23	0.18
Yellow Canary (*Crithagra flaviventris*)	17	29	0.23	0.17
Capped Wheatear (*Oenanthe pileata*)	25	21	0.07	0.19
Cape Wagtail (*Motacillia capensis*)	21	11	0.13	0.03
Karoo Korhaan (*Eupodotis vigorsii*)	1500	10	0.13	0.02
Nicholson's Pipit (*Anthus nicholsoni*)	30	9	0.02	0.09
African Pipit (*Anthus cinnamomeus*)	24.5	8	0.02	0.08
Familiar Chat (*Oenanthe familiaris*)	22	7	0	0.08
Cape Turtle Dove (*Streptopelia capicola*)	155	5	0.03	0.03
Secretarybird (*Sagittarius serpentarius*)	4000	5	0	0.06
Karoo Chat (*Emarginata schlegelii*)	32	3	0.02	0.02
Karoo Lark (*Calendulauda albescens*)	29	1	0.02	0
Mountain Wheatear (*Myrmecocichla monticola*)	35	1	0	0.01

Changes in the timing of bird visits in response to shade structures

A significant positive interaction was seen between phase and experimental treatment in the proportion of overall (structure and open bank cameras combined) bird visitations (all species combined) in the afternoon versus the morning (est. 1.51, SE = 0.52, P < 0.01, Table 6). This was reflected by a positive significant interaction between phase and experimental treatment in the proportion of birds visiting structure cameras in the afternoon versus the morning (est. 3.06, SE = 0.58, P < 0.01), but no significant interaction was seen at the open bank (See Table 6 for full model outputs). This suggests an increase in the proportion of birds visiting waterholes under structures in the afternoon in Phase 2 compared to Phase 1 at experimental waterholes (where shade was added to structures) relative to control waterholes (no shade added in Phase 2) (Figure 12).

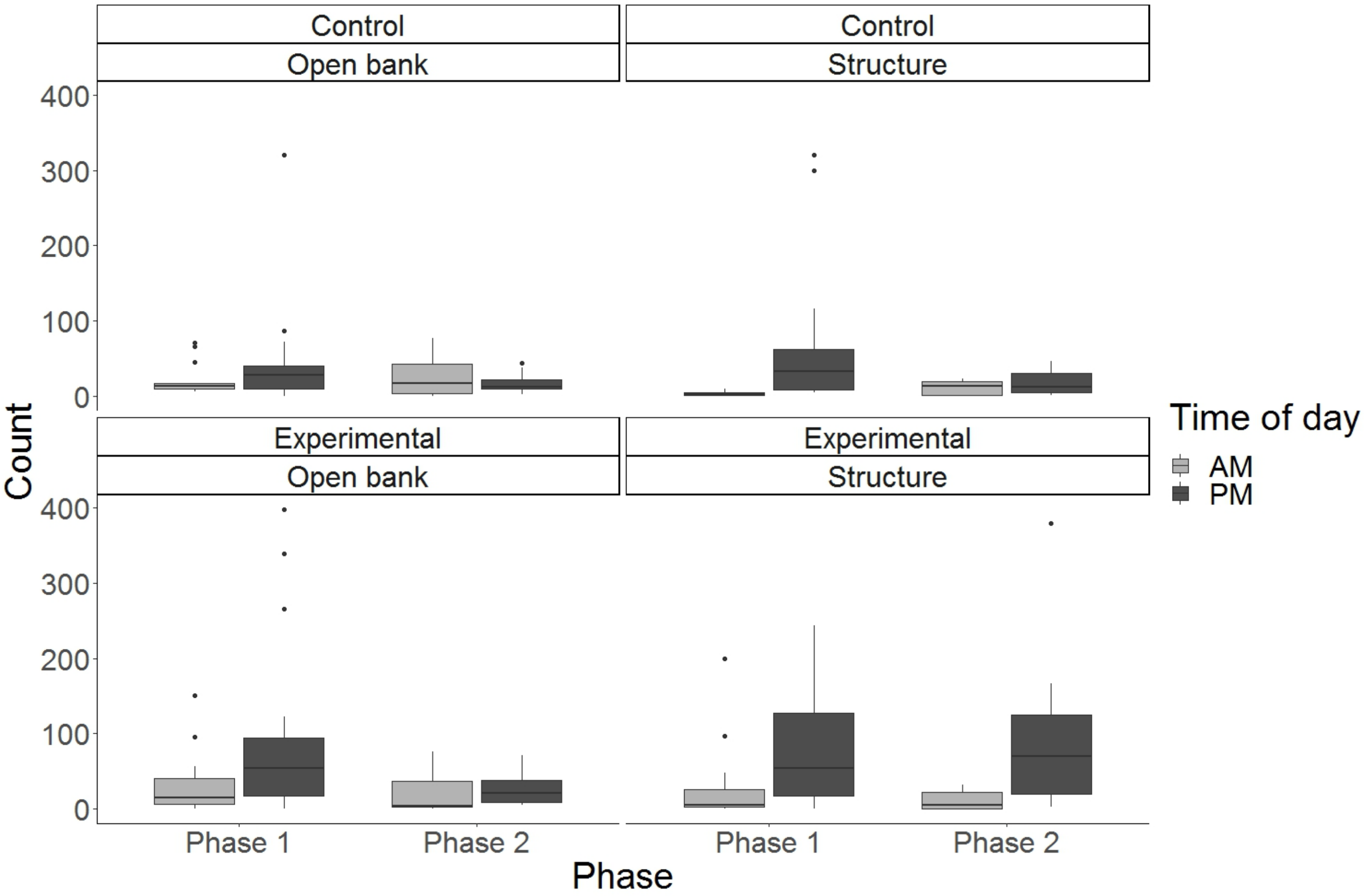


Figure 12: Overall species visits (all species combined) in the morning ('AM', dark grey) and afternoon ('PM', light grey) at the structure and open bank cameras for control and experimental waterholes. Boxplots show the median number of visits (central line), inter-quartile range (box edges), visitation range (whiskers) and outliers (black circles), including 3 control waterholes where no structures were shaded and 3 experimental waterholes where shade was provided in Phase 1 (pre-shading) and Phase 2 (shaded). Experimental structures in Phase 2 are seen to have significantly higher visits in the afternoon than morning compared with the experimental open bank, control open bank and control structures in Phase 2.

Table 6: Model outputs for the interaction between treatment (experimental: where no shade was added, vs control: where shade was added) and experimental phase (Phase 1: before shade was added, and Phase 2: after shade was added) on the proportion of birds visiting in the afternoon versus the morning (1) under structures (2) on open bank, and (3) overall (open bank and structure cameras combined). Models were GLMMs fitted with binomial distribution, waterhole and date were included as fixed effects as well as observation level random effects. Phase 1 and Treatment: control are set as baselines. Bold type indicates significant effects.

Response variable	Factor	Estimate	SE	Z-value	P-value
Proportion of birds visiting structures in the afternoon versus the morning	*Intercept*	***2.94***	***0.96***	***3.07***	***<0.01***
	Phase (Phase 2)	**-2.14**	**0.51**	**-4.19**	**<0.01**
	Treatment (Experimental)	-0.83	1.32	-0.63	0.53
	Treatment*Phase	**3.06**	**0.58**	**5.29**	**<0.01**
Proportion of birds visiting open bank in the afternoon versus the morning	*Intercept*	*0.40*	*0.48*	*0.83*	*0.40*
	Phase (Phase 2)	-0.40	0.38	-1.06	0.29
	Treatment (Experimental)	0.83	0.68	1.22	0.22
	Treatment*Phase	0.14	0.54	0.25	0.80
Proportion of birds visiting overall (structure and open bank cameras combined)in the afternoon versus the morning	*Intercept*	***1.50***	***0.67***	***2.23***	***0.03***
	Phase (Phase 2)	**-1.13**	**0.38**	**-2.99**	**0.03**
	Treatment (Experimental)	0.13	0.95	0.13	0.89
	Treatment*Phase	**1.51**	**0.52**	**2.89**	**<0.01**

Discussion

The aim of this study was to assess whether providing shade at waterholes could increase accessibility of water for desert birds during periods of high air temperature. The results were consistent with predictions that shade structures would significantly reduce operative temperatures at the water's edge in the afternoon and that bird visitation rates would therefore increase under the structures during the hottest parts of the day. However, the frequency of visitation by birds was species dependent. Trends in overall bird visitation rate were driven by four significantly-responding passerine species, two of which responded positively to the addition of shade (Grey-backed Sparrow-larks and Tractrac Chats) and two negatively (Cape Sparrows and White-throated Canaries). The addition of shade also resulted in a shift in the timing of birds' visits to water to the hotter part of the day (afternoon from 12:00-19:00). However, the addition of shade did not significantly alter the number of species making use of waterholes, suggesting adding shade did not make water accessible to birds that would not otherwise drink. These results point to the potential for shade structures to act as thermal refugia at the water's edge during the afternoon when air temperatures can exceed 40°C, thereby allowing continued drinking access to the desert birds of the Tankwa Karoo during extreme heat.

The addition of shade cloth to experimental shade structures in Phase 2 significantly reduced operative temperatures at the water's edge on average by more than 9°C during the hottest part of the day (afternoon from 12:00-19:00). Black bulb temperatures under shaded structures rarely exceeded 45°C and both the mean and median temperatures, at 32.1°C and 33.6° C, were well below average avian body temperature (~41-42°C). In contrast, black bulb temperatures under control structures (mean: 40.6 ± 5.77°C and median: 41.43°C), and on the open bank (mean: 41.9 ± 7°C and median: 48.12°C) regularly exceeded avian body temperature, peaking well over 50°C at all sites in Phase 2. Operative temperatures in these areas regularly exceeded the 46-54°C range of lethal heat tolerance limits attained under laboratory conditions for 29 passerine species (McKechnie *et al.,* 2021; McKechnie & Wolf, 2019; Whitfield *et al.,* 2015). This was consistent with previous data collected in the area (Orolowitz, 2020). The addition of shade at the water's edge in this study therefore reduced operative temperatures below the range of potentially lethal temperatures and also reduced the thermoregulatory demands placed on birds by operative temperatures above their body temperature (Gerson *et al.*, 2014). Shade structures therefore have the potential to keep water available to drinking birds into the future as local temperatures continue to increase (Appendix 1).

Small birds, e.g. most desert passerines, are vulnerable to changes in temperature due to high surface area to volume ratios, low thermal inertia (Fisher *et al.,* 1972; McKechnie *et al.,* 2012, 2021; Walsberg, 1993; Wolf and Walsberg, 1996; Smit *et al.,* 2019) and a limited capacity to store vital resources such as water (Albright *et al.,* 2016, Fisher *et al.,* 1972; Smit *et al.,* 2019; Wolf & Walsberg, 1996). Balancing hyperthermia and dehydration and the resultant water budgets occur at a scale of minutes to hours during hot weather (Albright *et al.,* 2016; Smit *et al.,* 2019; Wolf & Walsberg, 1996). Access to water during the hottest parts of the day, even for those species typically independent of water (Smit, 2013), is therefore likely to be more necessary with an increase in temperature (Appendix 1; IPCC, 2007,2011,2022). This is consistent with findings by McKechnie & Wolf (2010) who suggest that water demands between the hours of 12:00-18:00 could increase in desert birds by 47-95% in birds ranging from 5-500g by the year 2080. The results of this study suggest that lower operative temperatures associated with shade provision may allow desert birds to maintain water balance and by extension- maintain thermoregulatory functions throughout the day. This will likely become more important as global temperatures continue to rise (IPCC, 2007,2011,2022) threatening avian communities with mass mortality events, range shifts and community collapses (Albright *et al.,* 2017; Conradie *et al.,* 2019, 2020; Iknayan & Beissinger, 2018; McKechnie & Wolf, 2010, 2019; McKechnie *et al.,* 2012).

Consistent with the black bulb temperature results, there was an increase in overall bird visitation rate to shaded structures and a decline in visitation rate to control structures in the afternoon in Phase 2, after shade was added at experimental waterholes. In contrast, visitation increased at control structures and decreased at shaded structures in the morning. Visitation rates at open stretches of waterhole bank were not affected by the interaction between treatment and phase in the morning or the afternoon, and the overall visitation rate (both cameras combined for the full day) also showed no significant interaction between experimental treatment and phase on visitation rates. These findings are contrary to Abdu *et al.* (2018b) who found an overall decrease in the visitation rate of birds (all species combined) to shaded waterholes during a similar experiment in the Kalahari. They suggested that increased actual/perceived predation risk associated with the shade cloth, reducing the visibility of avian predators attacking from above (Hart et al., 2018), was the potential driver for the observed decline in visitation rate. Fisher *et al.* (1972) also suggest that diurnal avian predators are likely one of the primary selection pressures in the behavioral patterns of desert birds drinking at waterholes. It is therefore likely that the decreased visitation rate in the morning in this study was also due to some form of perceived or actual predation risk. Because of the habituation period allowed at all waterholes after shading and prior to the collection of visitation rate data, and because the decline was not seen overall at experimental waterholes, it is unlikely that the novelty of shade itself was causing the decline in morning visits found in this study. On cool mornings, birds are less likely to risk potential predation by drinking under structures (due to being less able to see approaching predators), particularly because there is no benefit (shade only reached the water's edge at/just after midday). When temperatures are higher in the afternoon the benefits provided by the lower operative temperatures in shade may outweigh this potential predation risk. Due to the limited observations of predators at waterholes during the study, combined with the relatively short duration of data collection (not long enough to assess behavioral changes in predators), I was unable to explore the effects of potential predation introduced by the structures.

The lack of any impact of the experiment on overall visitation rates to waterholes (all species and both cameras combined for the full day) suggest that the presence of shaded structures did not deter the overall bird community from waterholes entirely, despite the fact that some species apparently avoided the shade structures themselves in the morning. This is consistent with my species richness results which showed no significant impact of the experiment. Abdu *et al.,* (2018b) found that the decreased visitation rate to shaded structures was driven by larger bodied species responding negatively to the presence of artificial shade. They suggested that altering structure design and placement, for example by only shading a section of the water's edge (as I did in this study) may mitigate this issue and allow larger species to still make use of the waterhole (Abdu *et al.,* 2018b). This was consistent with my results on Namaqua Sandgrouse that showed no significant interaction between phase and treatment on their visitation rates. Species-specific responses by the most common species are however a clear driver of overall visitation rate patterns and to fully understand the patterns seen in this study it is important to understand the behaviour and ecology driving species-specific responses.

Species-specific responses

Overall changes in bird visitation rates to waterholes during this study were driven by four passerine species that significantly responded to the addition of artificial shade. Grey-backed Sparrow-larks and Tractrac Chats had a significant positive response, and White-throated Canaries and Cape Sparrows had a negative response to the addition of shade at experimental waterholes in Phase 2. Mean visitation rates to all waterholes by Grey-backed Sparrow-larks declined between Phase 1 and Phase 2. This can most likely be attributed to their nomadic lifestyle leading to a general decline in numbers present in the TKNP later in the study as the dry season progressed (Engelbrecht, 2017). This decline was buffered at experimental waterholes relative to control waterholes both on the open bank (indicated by a significant positive interaction between experimental treatment and phase), and overall, but not specifically at the shaded structure. Being a gregarious species, Grey-backed Sparrow-larks will typically travel and drink in groups (Engelbrecht, 2017). One hypothesis as to why the interaction between treatment and phase was significant overall and at the open bank camera, but not at the structure, is the limited available space under shading. Intraspecific competition caused by large groups may have limited access to the shade that had initially attracted the individuals, who then made use of the water source regardless, increasing the visitation rate at the open bank. Further study is required in this regard to fully understand this interaction.

Tractrac Chats are not known to be a drinking species but they were observed drinking in this study (Figure 13). This species showed an overall increase in visitation rates at experimental waterholes relative to a decrease at control waterholes in Phase 2 (i.e. a significant positive interaction between treatment and phase on overall visitation rates. This result was driven by a positive interaction between treatment and phase under the structures but no significant interaction was seen at the open bank. The increase in visitation rate at experimental waterholes and specifically under shade structures suggests that shade was a primary attractant for this species. The decline in Tractrac Chat visitation rates between Phase 1 and 2 at control waterholes might reflect the higher air temperatures during Phase 1 as even habitually non-drinking species will make use of surface water if temperature and thus thermoregulatory demands are high (Czenze *et al.,* 2020; Fisher *et al.,* 1972). However, once shade was available at experimental waterholes, Tractrac Chats seem to be choosing to make use of it. Although the chats were certainly drinking water at least some of the time (see Fig 13), it is hard to say for certain whether this species was seeking shade solely for the purpose of accessing the water, or whether this was an isolated behaviour by specific individuals, and this is discussed in the *Caveats and limitations* section below.

Figure 13: Tractrac Chats accessing and drinking water at the ‘Stonefence’ waterhole in the Tankwa Karoo National Park in January 2022.

Cape Sparrows and White-throated Canaries responded negatively to the addition of shade, as evidenced by significant negative interactions between treatment and phase on overall visitation rates by both species. For both species, there was overall increase in their visitation rate to water between Phase 1 and Phase 2, which may be a result of the reduced precipitation in Phase 2, decreasing the availability of other surface water sources. This background increase in visitation rates of Cape Sparrows was suppressed at experimental waterholes relative to control waterholes. A significant negative interaction between experimental treatment and phase on visitation rates at structures, open bank and overall suggested that this species was avoiding both the shaded structures and even experimental waterholes entirely. White-throated Canaries also showed an increase in overall visitation rates at control waterholes which was not reflected by an increase at experimental waterholes between Phase 1 and Phase 2. This was consistent with a significant negative interaction between experimental treatment and phase at structures, although the model for visitation rate at the open bank did not converge. These results again suggest that this species may also be avoiding both the shaded structures and experimental waterholes completely. White-throated Canaries were predominantly morning drinkers in both phases, whereas Cape Sparrows were predominantly afternoon drinkers in Phase 1 when temperatures were higher but drank slightly more frequently in the morning in Phase 2. The negative responses of both species can likely be attributed to the perceived/actual predation risk posed by the structures due to their obscuring of lines of sight for the birds from the water’s edge (Abdu et al., 2018b), combined with no shade at the water's edge and lower operative temperatures removing any benefit provided by the structures in the morning.

The differing responses of species to the addition of shade in this study suggest very different behaviours associated with when and why birds access water during the day. Fisher *et al.* (1972) found that drinking patterns are species-specific in Australian birds and this is likely to also be the case in African desert birds due to the similarity of evolutionary selective pressures associated with diet and size (Smit *et al.,* 2019). For example, granivorous species in desert environments are typically obligate drinkers while insectivorous species tend to be less reliant on surface water (Abdu *et al*., 2018b; Czenze *et al.,* 2020; Harrison *et al.,* 1997; Smit *et al*., 2019) and can therefore be classed broadly into occasional drinkers or non-drinking species (Czenze *et al.,* 2020). The species in this study that responded significantly to the addition of shade were primarily granivorous habitual drinkers with the exception of Tractrac Chats. During extreme high temperature conditions, thermoregulatory demands may force occasional and 'non-drinking' species like Tractrac Chats to drink in order to combat evaporative water loss (Czenze *et al.,* 2020). These species are unlikely to pre-emptively drink earlier in the day and may only access water to combat dehydration during periods of extreme heat (Czenze *et al.,* 2020). This would necessitate drinking during the hottest part of the day (when foraging is often also limited) and may explain the positive response to the structures seen in Tractrac Chats in Phase 2 of the experiment. It is also reflected by the majority of Tractrac Chat visitation observations occurring in the afternoon and is consistent with findings by Fisher et al (1972) who observed that non-drinking species did not tend to show a pattern of visitation and accessed water at any time of day if/when necessary. All of the significantly responding species in this study were of roughly the same size class (~17-27g) and size was not found to be a primary determining factor of response either positively or negatively (structure design had no impact on larger species) as it did in the Kalahari (Abdu *et al*., 2018b).

Consistent throughout the literature is that drinking habits and patterns of desert birds are strongly related to temperature (Abdu et al., 2018b; Conradie *et al.,* 2019; Fisher *et al.,* 1972; Lee *et al.,* 2017; McKechnie & Wolf, 2010; McKechnie et al., 2012, 2021; Smit *et al*., 2019) and may change as temperatures rise, suggesting the potential for shade structures to ultimately become more beneficial even for species that currently drink mostly in the morning. Drinking habits and patterns are flexible and have, for example, been seen to change across seasons (Bartholomew & Cade, 1963; Willoughbey & cade, 1967; Smyth & Bartholomew, 1966; Skead 1975). My results on the shift in the proportion of visitations in the afternoon versus the morning are consistent with this prediction. I found an increase in the proportion of birds visiting experimental structures in the afternoon (during the hottest parts of the day) versus the morning in Phase 2, relative to control structures where a decrease in the proportion of afternoon visits occurred. This was consistent with findings in the Kalahari (Abdu et al., 2018b) where a shift in the visitation patterns to the warmer parts of the day at shaded waterholes was seen. No significant interaction was found at the open bank, suggesting the presence of shade in Phase 2 allowed a shift in the time of visitations to the afternoon period when thermoregulatory demands were high. It is hard to say which species other than the two positively responding species made up this shift, though the majority of the species observed in this study were seen to have a higher overall visitation rate per hour in the afternoon than morning. Due to the reduced numbers of Grey-backed Sparrow-larks and Red-capped Larks, a greater proportion of the visitation rates were represented by other species in the study and it is therefore likely that the shift to afternoon drinking was driven by a combination of species in the area, highlighting the potential benefit of providing shade.

Caveats and study limitations

The primary limitation of this study was time and by extension sample size. Bird density in desolate areas like the Tankwa Karoo is significantly lower than areas like the Kalahari Desert. I observed only 9025 visitations compared to 43 507 visits seen by Abdu *et al.* (2018b) in a similar time frame. I needed to collect my data during periods of high heat in order to test the efficacy of shade structures in allowing access to water under such conditions. Air temperature and precipitation both decreased as summer progressed and waterholes began to dry up, limiting the duration in which relevant data could be collected. This short timeframe necessitated a BACI experimental design rather than a full-factorial design. Although a successful method (Green, 1979; Skalski & Robson, 2012; Abdu *et al.,* 2018; this study), I suggest that future studies attempt to collect more data over a longer period, perhaps over multiple summer seasons. This would increase the number of recorded bird visitations overall as well as per species, and would allow each waterhole to be provided with shade for part of the time in a fully-balanced design which could better control for habitat differences between waterholes. The increased sample size would improve statistical power and may allow for a better understanding of the impacts artificial shade has on more than just the four responding species seen in this study. A longer-term dataset that included multiple seasons, broader temperature ranges and broader habitat sampling may also yield a better understanding of the TKNP bird community's response to the provision of shade at the water's edge in the afternoon. This would also allow for the study of behavioral shifts at structures related to temperature changes, predation risk and the use of structures by species other than those intended (baboons and some larger birds of prey were observed making use of the structures for shade and as vantage points on occasion). Ideally future studies should include more waterholes, if possible, to increase the number of replicates and the statistical power to detect effects. This is however unlikely to be feasible in the Tankwa Karoo National Park due to the nature of the study site and the predicted impacts of climate change. For this area, one may have to settle for a longer study period. Perhaps increasing the study area to include permanent water sources outside the boundaries of the protected area would remedy this and this avenue should be explored in future studies.

The intricacies of species-specific responses with regards to waterhole-specific habitats and micro-climates may also be better understood from a long-term dataset. Interestingly, each of the four responding species appeared to visit specific waterholes more frequently than other waterholes. Local habitat appears to be the driver for this and seems to play an important part in the bird community composition at waterholes. This is of particular consequence in a diverse landscape, characterised by multiple microhabitats, such as the TKNP (Steyn et al., 2013). For example, 77.5% of Grey-backed Sparrow-lark visits occurred at the Abrahamsknee waterhole. This waterhole was located in an area characterised by large arid grasslands typical of habitat occupied by this species (Engelbrecht, 2017). The overall decline in Grey-backed Sparrow-lark population numbers may therefore have been buffered in this area due to the desirable local habitat. This species may then have been making use of the nearest available water source in this area which happened to be the experimental Abramsknee waterhole. Similarly, White-throated Canaries (72.4% of observations at Perdekop) and Cape Sparrows (57.8% of observations at Varschfontein) were found in areas either on the edge of the riparian zone of the Tankwa river (Perdekop) or near stands of alien vegetation and reeds which were observed to be nesting sites for species including Cape Sparrows (Varschfontein). All Tractrac Chats observed in this study were captured in images from either Varschfontein or Stonefence waterholes which were located in sparsely vegetated habitats (except for the reeds and some alien trees near Varschfontein). An effort was made to pair waterholes based on such factors and together with the BACI design of this study, I was still able to draw conclusions on the effects of adding artificial shade on the visitation rate of these species. I do however suggest that future studies try to incorporate a larger study area with a better spread of both control and experimental waterholes within a greater number of habitats/micro habitats in order to better assess the influence of shade structures at a species-specific level.

Another potential limitation to this study is that it was never clear whether all birds at the water's edge were actually there to drink. This is exemplified by Tractrac Chats' use of water at waterholes. Although observed drinking (Figure 13), it cannot be said in certainty that Tractrac Chats were making use of shade solely for rehydration. It is also likely that they were making use of the shade provided by structures as a thermal refuge given the high temperatures and sparsely vegetated nature of the area in which these two waterholes (and Tractrac Chats in general) were located. Another hypothesis is that, as well as allowing access to the water's edge for drinking, the shade provided at experimental sites may have attracted insects taking advantage of the thermal refuge themselves, thereby providing a food source. This is consistent with field observations as well as literature (Box *et al.,* 2008) that suggests waterholes, particularly in arid areas, may provide refuge to invertebrates. This food source was potentially unavailable to Tractrac Chats during the heat of the day before shade was provided. Further study in this regard is required, but whether the shade was providing direct access to water or a combination of water access and access to prey high in water content, the outcome and benefit are the same with the regards to the function of the artificial shade from the perspective of this study. Perhaps further research could be done on the influence of increased Tractrac Chat presence at waterholes (and the associated predation) on the invertebrate communities at arid waterholes. Birds were only counted if they were within 1m of the water's edge in an attempt to manage this limitation by increasing the probability that they were either drinking or enroute to or from the water. Red-capped Larks however were observed digging into the substrate, potentially to thermoregulate against the cooler wet sediment below the surface, and therefore present another alternative reason for being near the water's edge during the heat of the day.

The observed behaviours of Tractrac Chats and Red-capped Larks highlight a further limitation with regards to visitation rates. Because I was unable to identify individuals of any given species, visitation rate was used as a metric for 'intensity of use' and as such I was unable to distinguish between repeat visits by the same individuals or repeat counts of individuals that stayed long at the water's edge, and new visits by new individuals. It was therefore not possible to assess whether visitation patterns and drinking habits were isolated repeated behaviours by a few individuals, as may potentially have been the case for the Tractrac Chats seen drinking. Repeat counts of individuals that spent a long time in the shade or at the water's edge, like Red-capped Larks for example, may have also led to an overestimation of visitation rates for that species, introducing some level of uncertainty in the actual number of visitations by any given species. This did not ultimately impact the results as the experimental design meant I was looking at the change in visitation rates between the two phases rather than the absolute values of visitation in either phase. Consistent data capture from camera images therefore helped to mitigate this potential limitation in this study.

Management implications

It is my hope that this research can act as a pilot study for providing artificial shade at the water's edge in the TKNP and potentially all of South Africa's arid parks. This study is also well timed as TKNP began its 10-yearly Park Management Plan revision in 2021 and I hope that this research will aid in developing a Climate Change Adaptation Plan for this and other arid protected areas by raising reserve managements' awareness of the likely impacts of climate change on desert bird communities; given catastrophic mortality events and community collapses already taking place in other arid regions around the world (Albright *et al.,* 2017; Conradie *et al.,* 2019, 2020; McKechnie & Wolf, 2010, 2019; McKechnie *et al.,* 2012). I hope therefore to raise awareness of the potential strategies available to address these issues. Species such as Tractrac Chats and Grey-backed Sparrow-larks, being near endemics of arid-semiarid habitats in South Africa, are also of primary conservation concern and the positive response to artificial shade in this study highlights the importance of proactive climate change adaptation strategies to conserve these and other species in the arid protected areas of the country.

The shader design, with particular reference to shading only a section of the water's edge, appears to at least partially mitigate the negative effects observed by Abdu *et al.* (2018b) on the visitation rate of larger species. This, and the potential predation risks associated with structures, will need to be closely monitored in the long-term and as such I suggest that the structures I have erected in TKNP be incorporated into a longer-term monitoring and evaluation plan. This will also allow for a better understanding of the species-specific benefits or shortfalls of the provision of artificial shade at waterholes. Shade structures of this design, if adopted, could be constructed out of longer lasting materials (such as steel frames) in the same style and would require little to no maintenance. Shade cloth could potentially be put onto these frames in the summer and removed in the winter, thereby limiting any negative effects the shade may have on birds during cooler temperatures. Structures could also be put up on a habitat-specific basis and shade could be added only during extreme heatwaves in habitats occupied by currently negatively-responding species. The structure design is thus versatile and could be used preemptively based on weather predictions or permanently at specific waterholes.

Conclusions

Providing artificial shade successfully buffers the effects of high temperatures by maintaining birds' overall visitation rates to the water's edge during periods of extreme heat. Structures at the water's edge provided sufficient shade in the afternoon to reduce operative temperatures away from lethal thermal limits for many small passerine species. Overall bird visitation rates increased beneath structures in the afternoon in response to the addition of shade but decreased in the morning, likely due to a perceived/actual predation risk while operative temperatures were low and structures provided no thermal benefit. Species richness was unaffected by the presence of artificial shade and both positive and negative responses to shade were seen to be species-specific, with arid zone specialists; Grey-back Sparrow-larks and Tractrac Chats responding positively. There was an observed shift in overall bird visitation rates from the morning to the afternoon at shaded structures, suggesting temperature as a primary driver in the use of shade. As temperatures increase in deserts such as the Tankwa Karoo due to the effects of climate change (IPCC, 2007,2011,2022), thermoregulatory demands are likely to necessitate drinking at hotter times of day that may differ from the normal habits of many species. It seems apparent that species in the TKNP and other arid areas may be forced to drink more in the afternoon as air temperatures continue to increase. Structures providing access to surface water during the heat of the afternoon will likely become more desirable to even those species that were seen to negatively respond in this study. Further research and monitoring are required to understand the responses of a broader range of species to the provision of shade, to make decisions on the location of structures in diverse habitats and to observe behavioral changes in response to the presence of shade.

References

Abdu, S., Lee, A. T., & Cunningham, S. J. (2018a). The presence of artificial water points structures an arid-zone avian community over small spatial scales. *Ostrich*, *89*(4), 339-346.

Abdu, S., McKechnie, A. E., Lee, A. T., & Cunningham, S. J. (2018b). Can providing shade at water points help Kalahari birds beat the heat? *Journal of Arid Environments*, *152*, 21-27.

Albright, T. P., Mutiibwa, D., Gerson, A. R., Smith, E. K., Talbot, W. A., O'Neill, J. J., McKechnie, A. E. & Wolf, B. O. (2017). Mapping evaporative water loss in desert passerines reveals an expanding threat of lethal dehydration. *Proceedings of the National Academy of Sciences*, *114*(9), 2283-2288.

Archer, S. R., & Predick, K. I. (2008). Climate change and ecosystems of the southwestern United States. *Rangelands*, *30*(3), 23-28.

Bakken, G. S., Santee, W. R., & Erskine, D. J. (1985). Operative and standard operative temperature: tools for thermal energetics studies. *American Zoologist*, *25*(4), 933-943.

Bates, D., Maechler, M., Bolker, B., Walker, S. (2015). Fitting LinearMixed-Effects Models Using lme4. Journal of Statistical Software, 67(1), 1-48.doi:10.18637/jss.v067.i01.

Bartholomew, G. A., & Cade, T. J. (1963). The water economy of land birds. *The Auk*, *80*(4), 504-539.

Box, J. B., Duguid, A., Read, R. E., Kimber, R. G., Knapton, A., Davis, J., & Bowland, A. E. (2008). Central Australian waterbodies: the importance of permanence in a desert landscape. *Journal of Arid Environments*, *72*(8), 1395-1413.

Cade, T. J. (1965). Relations between raptors and columbiform birds at a desert water hole. *The Wilson Bulletin*, *77*(4), 340-345.

Conradie, S. R., Woodborne, S. M., Cunningham, S. J., & McKechnie, A. E. (2019). Chronic, sublethal effects of high temperatures will cause severe declines in southern African arid-zone birds during the 21st century. *Proceedings of the National Academy of Sciences*, *116*(28), 14065-14070.

Conradie, S. R., Woodborne, S. M., Wolf, B. O., Pessato, A., Mariette, M. M., & McKechnie, A. E. (2020). Avian mortality risk during heat waves will increase greatly in arid Australia during the 21st century. *Conservation Physiology*, *8*(1), coaa048.

Cooper, C. E., Withers, P. C., Hurley, L. L., & Griffith, S. C. (2019). The field metabolic rate, water turnover, and feeding and drinking behavior of a small avian desert granivore during a summer heatwave. *Frontiers in Physiology*, 1405.

Czenze, Z. J., Kemp, R., Van Jaarsveld, B., Freeman, M. T., Smit, B., Wolf, B. O., & McKechnie, A. E. (2020). Regularly drinking desert birds have greater evaporative cooling capacity and higher heat tolerance limits than non-drinking species. *Functional Ecology*, *34*(8), 1589-1600.

Davies, S. J. J. F. (1982). Behavioural adaptations of birds to environments where evaporation is high and water is in short supply. *Comparative Biochemistry and Physiology Part A: Physiology*, *71*(4), 557-566.

Dean, W. R. J. (1995). Where birds are rare or fill the air: the protection of the endemic and the nomadic avifaunas of the Karoo. (PhD Thesis). University of Cape Town, Cape Town. Retrieved from: https://open.uct.ac.za/handle/11427/9674

Dean, W. R. J., & Williams, J. B. (2004). Adaptations of birds for life in deserts with particular reference to larks (Alaudidae). *Transactions of the Royal Society of South Africa*, *59*(2), 79-91.

Desmet, P. G., Cowling, R. M., Ellis, A. G., & Pressey, R. L. (2002). Integrating biosystematic data into conservation planning: perspectives from southern Africa's Succulent Karoo. *Systematic Biology*, *51*(2), 317-330.

du Plessis, K. L., Martin, R. O., Hockey, P. A., Cunningham, S. J., & Ridley, A. R. (2012). The costs of keeping cool in a warming world: implications of high temperatures for foraging, thermoregulation and body condition of an arid-zone bird. *Global Change Biology*, *18*(10), 3063-3070.

Engelbrecht, D. (2017). How the east was won: breeding range extension of the Grey-backed Sparrow-lark *Eremopterix verticalis. Biodiversity Observations*, *8*, 34-1.

Engelbrecht, F., Adegoke, J., Bopape, M. J., Naidoo, M., Garland, R., Thatcher, M., ... & Gatebe, C. (2015). Projections of rapidly rising surface temperatures over Africa under low mitigation. *Environmental Research Letters*, *10*(8), 085004.

Ferns, P. N., & Hinsley, S. A. (1995). Importance of topography in the selection of drinking sites by sandgrouse. *Functional Ecology*, 371-375.

Fisher, C. D., Lindgren, E., & Dawson, W. R. (1972). Drinking patterns and behavior of Australian desert birds in relation to their ecology and abundance. *The Condor*, *74*(2), 111-136.

Fox, J. (2003). Effect Displays in R for Generalised Linear Models. Journal of Statistical Software, 8(15), 1-27. URL https://www.jstatsoft.org/article/view/v008i15.

Gerson, A. R., Smith, E. K., Smit, B., McKechnie, A. E., & Wolf, B. O. (2014). The impact of humidity on evaporative cooling in small desert birds exposed to high air temperatures. *Physiological and Biochemical Zoology*, *87*(6), 782-795.

Giorgi, F., & Bi, X. (2005). Updated regional precipitation and temperature changes for the 21st century from ensembles of recent AOGCM simulations. *Geophysical Research Letters*, *32*(21).

Green, R. H. (1979). *Sampling design and statistical methods for environmental biologists*. John Wiley & Sons, New York.

Harrison, J. A., & Cherry, M. (1997). The atlas of southern African birds. *Nature*, *389*(6646), 32-32.

Harrison, J. A., & Cherry, M. (1997). The atlas of southern African birds. *Nature*, *389*(6646), 32-32

Harrison, X. A. (2014). Using observation-level random effects to model overdispersion in count data in ecology and evolution. *PeerJ*, *2*, e616.

Hart, L. A., Wreford, E. P., Brown, M., & Downs, C. T. (2018). Hunting flight speeds of five southern African raptors. *Ostrich*, *89*(3), 251-258.

Hervé, M. (2022). RVAideMemoire: Testing and Plotting Procedures for Biostatistics. R package version 0.9-81-2. https://CRAN.R-project.org/package=RVAideMemoire

Hilbe, J. M. (2011). *Negative binomial regression*. Cambridge University Press, Cambridge.

Iknayan, K. J., & Beissinger, S. R. (2018). Collapse of a desert bird community over the past century driven by climate change. *Proceedings of the National Academy of Sciences*, *115*(34), 8597-8602.

IPCC, 2022: *Climate Change 2022: Impacts, Adaptation, and Vulnerability.*Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [H.-O. Pörtner, D.C. Roberts, M. Tignor, E.S. Poloczanska, K. Mintenbeck, A. Alegría, M. Craig, S. Langsdorf, S. Löschke, V. Möller, A. Okem, B. Rama (eds.)]. Cambridge University Press. In Press.

IPCC, 2011: IPCC Spe-cial Report on Renew-able Energy Sources and Cli-mate Change Mitigation. Prepared by Working Group III of the Intergovernmental Panel on Climate Change [O. Eden-hofer, R. Pichs-Madruga, Y. Sokona, K. Sey-both, P. Matschoss, S. Kadner, T. Zwickel, P. Eickemeier, G. Hansen, S. Schlömer, C. von Stechow (eds)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 1075 pp.

IPCC, 2007: Climate Change 2007: Synthesis Report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, Pachauri, R.K and Reisinger, A. (eds.)]. IPCC, Geneva, Switzerland, 104 pp.

Kemp, R., Freeman, M. T., van Jaarsveld, B., Czenze, Z. J., Conradie, S. R., & McKechnie, A. E. (2020). Sublethal fitness costs of chronic exposure to hot weather vary between sexes in a threatened desert lark. *Emu-Austral Ornithology*, *120*(3), 216-229.

Lee, A. T. K., & Wright, D. R. (2020). Patterns of bird species richness at two sampling scales in the Karoo biome of South Africa. *Journal of Arid Environments*, *174*, 104077.

Lee, A. T., Wright, D., & Barnard, P. (2017). Hot bird drinking patterns: drivers of water visitation in a fynbos bird community. *African Journal of Ecology*, *55*(4), 541-553.

Lee, A. T., Geary, C., Wright, D. R., & Dean, W. R. J. (2019). Vulnerability of birds to contaminated water sources in the Karoo region of South Africa. *Ostrich*, *90*(4), 397-406.

Lenth, R.V. (2021). emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.7.0. https://CRAN.R-project.org/package=emmeans

Le Roux, P. C., & McGeoch, M. A. (2008). Changes in climate extremes, variability and signature on sub-Antarctic Marion Island. *Climatic change*, *86*(3), 309-329.

Levy, O., Dayan, T., Porter, W. P., & Kronfeld-Schor, N. (2016). Foraging activity pattern is shaped by water loss rates in a diurnal desert rodent. *The American Naturalist*, *188*(2), 205-218.

Maclean, G. L. (1983). Water transport by sandgrouse. *Bioscience*, *33*(6), 365-369.

Maclean, G. L. (1996). *Ecophysiology of desert birds*. Springer Science & Business Media, Berlin.

MacMillen, R. E. (1990). Water economy of granivorous birds: a predictive model. *The Condor*, *92*(2), 379-392.

MacMillen, R. E., & Baudinette, R. V. (1993). Water economy of granivorous birds: Australian parrots. *Functional Ecology*, 704-712.

Maggs, G. L., Craven, P., & Kolberg, H. H. (1998). Plant species richness, endemism, and genetic resources in Namibia. *Biodiversity & Conservation*, *7*(4), 435-446.

Major, J. (1988). Endemism: a botanical perspective. In *Analytical biogeography* (pp. 117-146). Springer, Dordrecht.

Mbokodo, I., Bopape, M. J., Chikoore, H., Engelbrecht, F., & Nethengwe, N. (2020). Heatwaves in the future warmer climate of South Africa. *Atmosphere*, *11*(7), 712.

McKechnie, A. E., Gerson, A. R., & Wolf, B. O. (2021). Thermoregulation in desert birds: scaling and phylogenetic variation in heat tolerance and evaporative cooling. *Journal of Experimental Biology*, *224*(Suppl_1), jeb229211.

McKechnie, A. E., Hockey, P. A., & Wolf, B. O. (2012). Feeling the heat: Australian landbirds and climate change. *Emu-Austral Ornithology*, *112*(2), i-vii.

McKechnie, A. E., & Wolf, B. O. (2010). Climate change increases the likelihood of catastrophic avian mortality events during extreme heat waves. *Biology Letters*, *6*(2), 253-256.

McKechnie, A. E., & Wolf, B. O. (2019). The physiology of heat tolerance in small endotherms. *Physiology*, *34*(5), 302-313.

Moore, D., Stow, A., & Kearney, M. R. (2018). Under the weather?—The direct effects of climate warming on a threatened desert lizard are mediated by their activity phase and burrow system. *Journal of Animal Ecology*, *87*(3), 660-671.

Nunez, S., Arets, E., Alkemade, R., Verwer, C., & Leemans, R. (2019). Assessing the impacts of climate change on biodiversity: is below 2° C enough?. *Climatic Change*, *154*(3), 351-365.

Orolowitz, M. (2020). *Life on the edge: do body size and drinking dependency influence how birds deal with the heat in South Africa's most extreme desert?*. (Master Thesis). University of Cape Town. Retrieved from http://hdl.handle.net/11427/32497

Randall, J. A. (1993). Behavioural adaptations of desert rodents (Heteromyidae). *Animal Behaviour*, *45*(2), 263-287.

Riddell, E. A., Iknayan, K. J., Wolf, B. O., Sinervo, B., & Beissinger, S. R. (2019). Cooling requirements fueled the collapse of a desert bird community from climate change. *Proceedings of the National Academy of Sciences*, *116*(43), 21609-21615.

Rubin, F. (1998). The physical environment and major plant communities of the Tankwa-Karoo National Park. *Koedoe*, *41*(2), 61-94.

Ruth, J. M., Talbot, W. A., & Smith, E. K. (2020). Behavioral response to high temperatures in a desert grassland bird: use of shrubs as thermal refugia. *Western North American Naturalist*, *80*(2), 265-275.

SANParks, © SANParks 2004 - 2022.Tankwa Karoo National Park. Vital Information. https://www.sanparks.org/parks/tankwa/tourism/general.php Accessed August 2022

SANParks (2014) Tankwa Karoo National Park: Park Management Plan 2014-2024. SANParks, Pretoria.

Schmidt-Nielsen, K. (1964). Desert animals. Physiological problems of heat and water. *Desert animals. Physiological problems of heat and water,* Claredon press, Oxford.

Skalski, J. R., & Robson, D. S. (2012). *Techniques in wildlife investigations: design and analysis of capture data*. Academic Press, New York.

Skead, D. M. (1975). Drinking habits of birds in the central Transvaal bushveld. *Ostrich*, *46*(2), 139-146.

Smit, B. (2013). *Taking the heat: integrating behavioural and physiological variables to predict avian responses to climate change in the Kalahari Desert* (Doctoral dissertation, University of Pretoria).

Smit, B., Woodborne, S., Wolf, B. O., & McKechnie, A. E. (2019). Differences in the use of surface water resources by desert birds are revealed using isotopic tracers. *The Auk*, *136*(1), uky005.

Smith, E. K., O'Neill, J. J., Gerson, A. R., McKechnie, A. E., & Wolf, B. O. (2017). Avian thermoregulation in the heat: resting metabolism, evaporative cooling and heat tolerance in Sonoran Desert songbirds. *Journal of Experimental Biology*, *220*(18), 3290-3300.

Smyth, M., & Bartholomew, G. A. (1966). The water economy of the Black-throated Sparrow and the Rock Wren. *The Condor*, *68*(5), 447-458.

Steyn, H. M., Bester, S. P., & Bezuidenhout, H. (2013). An updated plant checklist for Tankwa Karoo National Park, South Africa. *South African Journal of Botany*, *88*, 247-251.

Suárez, A., Watson, R. T., & Dokken, D. J. (2002). Climate change and biodiversity.

Van der Merwe, H., Bezuidenhout, H., & Bradshaw, P. L. (2015). Landscape unit concept enabling management of a large conservation area: A case study of Tankwa Karoo National Park, South Africa. *South African Journal of Botany*, *99*, 44-53.

Van de Ven, T. M., McKechnie, A. E., & Cunningham, S. (2019). The costs of keeping cool: behavioural trade-offs between foraging and thermoregulation are associated with significant mass losses in an arid-zone bird. *Oecologia*, *191*(1), 205-215.

van Wilgen, N. J., Goodall, V., Holness, S., Chown, S. L., & McGeoch, M. A. (2016). Rising temperatures and changing rainfall patterns in South Africa's national parks. *International Journal of Climatology*, *36*(2), 706-721.

Venables, W. N. & Ripley, B. D. (2002) Modern Applied Statistics with S. Fourth Edition. Springer, New York. ISBN 0-387-95457-0.

Walsberg, G. E. (1993). Thermal consequences of diurnal microhabitat selection in a small bird. *Ornis Scandinavica*, 174-182.

Whitfield, M. C., Smit, B., McKechnie, A. E., & Wolf, B. O. (2015). Avian thermoregulation in the heat: scaling of heat tolerance and evaporative cooling capacity in three southern African arid-zone passerines. *The Journal of Experimental Biology*, *218*(11), 1705-1714.

Wickham et al., (2019). Welcome to the tidyverse. Journal of Open Source Software, 4(43), 1686, https://doi.org/10.21105/joss.01686

Willoughby, E. J., & Cade, T. J. (1967). *Drinking habits of birds in the central Namib Desert of South West Africa*. Namib Desert research Association, Windhoek.

Wolf, B. O., & Walsberg, G. E. (1996a). Thermal effects of radiation and wind on a small bird and implications for microsite selection. *Ecology*, *77*(7), 2228-2236.

Wolf, B. O., & Walsberg, G. E. (1996b). Respiratory and cutaneous evaporative water loss at high environmental temperatures in a small bird. *The Journal of Experimental Biology*, *199*(2), 451-457.

Appendix 1

Mean maximum daily air temperature in the study area over a period of three decades has increased at a rate of 0.034° per year (F = 14.36, df = 33, $R^2 = 0.03$) resulting in an overall increase of 1.16°C in 34 years (Figure 14).

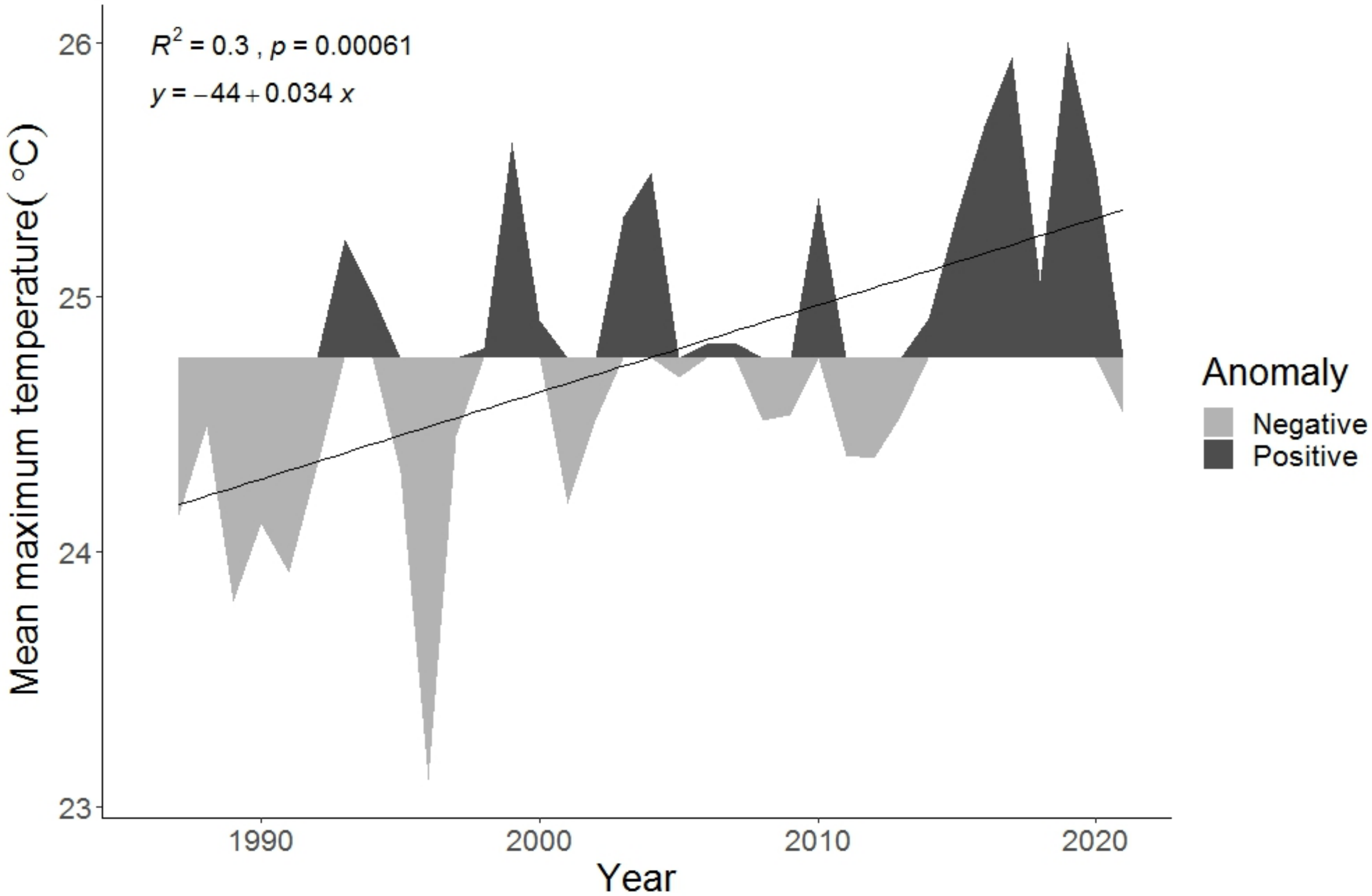


Figure A1: Mean daily maximum temperature from the Calvinia weather station (~100km NW of the TKNP) showing the annual difference from the mean maximum temperature for the period 1987-2021 ('Anomaly'). Trend line shows the increase in mean daily maximum temperature 0.034°C per year over this period. Data were provided by the South African Weather Service (SAWS).