



**HOME RANGE AND THERMAL ANALYSES OF TWO
SYMPATRIC TORTOISE SPECIES, *STIGMOCHELYS
PARDALIS* AND *PSAMMOBATES OCULIFER* IN THE
THORNBUSH SAVANNA OF CENTRAL NAMIBIA.**

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DECLARATION

I, Klaudia Kiinge Amutenya, hereby declares that the work contained in the thesis, entitled “Home Range and Thermal Analyses of Two Sympatric Tortoise Species, *Stigmochelys pardalis* and *Psammobates oculifer* in the Thorn-bush Savannah of central Namibia” is my own original work and that I have not previously in its entirety or in part submitted it at any university or other higher education institution for the award of a degree.

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ABSTRACT

Southern Africa harbors one-third of the world's Testudinid species, many of which inhabit arid or semi-arid areas. Namibia has the second highest tortoise diversity after South Africa with six species and five of the recognized genera of modern Testudinidae in the world. Detailed ecological information on the Namibian species is generally lacking. This study analyzed the home ranges and thermal activities of two sympatric tortoise species, the Leopard tortoise, *Stigmochelys pardalis* (previously known as *Geochelone pardalis*) and the poorly studied Kalahari tent tortoise, *Psammobates oculifer*. The study was conducted at the Hohewarte Farm, situated in the thorn-bush savanna southwest of Windhoek, Namibia. All encountered tortoises from both species were equipped with radio transmitters and temperature loggers (iButtons) which allowed for continuous monitoring of individuals throughout the study period. Data was collected for 17 months from December 2013 to April 2015 to determine the average annual and seasonal difference in thermally driven activity patterns and home range of these tortoises. Results from the study suggest that the smaller *P. oculifer* (with one dramatic exception of a wandering male) had a larger average annual home range (64 ha) compared to the much larger and common *S. pardalis* (20 ha). Exclusion of the wandering male from data analysis yielded a reduction in the annual home range size of *P. oculifer* to 32 ha. There was however great variation within individual home range sizes; the largest annual home range size (299 ha) was for a male *P. oculifer* while the smallest annual average home range was 5 ha recorded for two (2) female *P. oculifer*. For *S. pardalis*, 58 ha was the largest annual average home range size recorded for a medium sized male while two (2) juvenile *S. pardalis* had the smallest annual average home ranges of 1 ha. The study also found that home ranges were larger during the wet seasons for both species and that there was evident intraspecific and interspecific home range overlaps between the two species and even between sexes of the same species. There was no significant difference found between the different temperatures recorded for the tortoises (shell, iButton, ambient and surface). On the orientation aspect of the study, tortoise rear orientation directions differed and were not uniform. Results from Rayleigh's Z statistical test (Rayleigh Z7.075, $P < 0.001$) have shown that there was no mean direction for the species orientation. It was however found that during the dry season, the northerly directions (NE and NW) were the dominant rear directions for *S. pardalis* while N, NE, and easterly direction (E) were the dominant rear directions for *P. oculifer*. Observations during the wet seasons have indicated that

S. pardalis tortoises mostly oriented their rear end towards the NE and N directions while the westerly directions (NW, W, and SW) were the dominant directions for *P. oculifer*. The NE direction was observed to be the mean direction that tortoises from both species oriented the rear ends towards.

Key words: Sympatric, tortoises, *Psammobates oculifer*, *Stigmochelys pardalis*, home range, thermal activities, orientation, wet season, dry season.

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All maps, graphs and tables presented in this thesis were produced by the author, unless otherwise stated.

ABBREVIATIONS

P. oculifer = *Psammobates oculifer*

S. pardalis = *Stigmochelys pardalis*

Psoc = *Psammobates oculifer*

Stpa = *Stigmochelys pardalis*

N = North

NE = North-east

E = East

SE = South-east

S = South

SW = South-west

W = West

NW = North-west

F = Female

M = Male

J = Juvenile

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“When the well is dry, we know the worth of water”

-Benjamin Franklin

1. INTRODUCTION

1.1 General Introduction

Tortoises are reptiles that are categorized into the order Chelonian and family Testudinidae. Chelonians are among the oldest vertebrates that exist today, having changed little in their general appearance since they evolved during the Mesozoic era, roughly 200 million years ago (Campbell, 1990). Branch (1998) used the wordings “shielded reptiles” to refer to all tortoises as they are easily recognized by their shell and cannot be mistaken for any other reptiles.

There are roughly 45 described terrestrial tortoise species that are widely distributed around the world. According to Keswick (2012), southern Africa alone comprises one-third (15) of the total world tortoise species, many of which inhabit arid or semi-arid areas. Namibia is second only to South Africa in terms of total tortoise species richness with 6 species and 5 of the recognized genera of recent Testudinidae in the world (Griffin, 2000). However, despite all tortoises in southern Africa being listed on CITES Appendix II species, very little is known about their ecology (Boycott & Bourquin, 2000).

The second highest tortoise diversity places Namibia as an important country in the ongoing conservation of tortoises. Two of the most widespread Namibian tortoise species are the Leopard tortoise (*Stigmochelys pardalis*, Bell, 1828), previously placed in the genus *Geochelone* (Fritz & Havas, 2006) and the Kalahari Tent tortoise (*Psammobates oculifer*, Kuhl, 1820), see Figure 1. Other species in Namibia include the Bushman-land tent tortoise (*Psammobates tentorius verroxii*, Bell, 1828), the Namaqualand tent tortoise (*Psammobates tentorius trimeni*, Bell, 1828), the Hinged tortoise (*Kinixyx spekii*, Gray, 1863), the Bowsprit angulate tortoise (*Chersina angulate*, Schweigger, 1812), and the Nama padloper (*Homopus solus*, Branch, 2007). *Homopus solus* is endemic to Namibia with a restricted distribution and is listed on the International Union for Conservation of Nature (IUCN Red List) as “Vulnerable” (Alexander & Marais, 2007).



FIGURE 1. The Leopard tortoise, *S. pardalis* (left) and Kalahari tent tortoise, *P. oculifer* (right) are widely distributed in the savanna and semi-arid environments of Namibia.

Stigmochelys pardalis and *P. oculifer* tortoises exhibit significantly different physical characteristics and often occur sympatrically at the landscape scale. The genus *Stigmochelys* includes only one single species, *S. pardalis* which is the largest tortoise species in southern Africa. The common name is derived from its leopard like patterns and it is the most widely distributed tortoise species in Namibia, only absent in the extremely dry western coastal and sandy Namib Desert regions (Cunningham, 2005). McMaster & Dawn (2013) state that this species is territorial and roams over large areas in search of food, water and potential mates, and their home ranges can exceed 80 hectares (ha) (Alexander & Marais, 2007). In Namibia, *S. pardalis* favours a variety of habitats including the dry dwarf shrub savanna in the south, the sandy savannah in the east, the highlands and thorn-bush in the central regions, as well as the mopane and dry woodland savanna in the far north-east (Cunningham, 2005).

The *Psammobates* ('sand loving') genus is an arid or semi-arid dwelling genus (with the exception of *P. geometricus*) (Keswick, 2012) which is endemic to southern

Africa and occurs throughout the central and southern Kalahari regions of South Africa, Namibia and Botswana (Boycott & Bourquin, 2000; Branch, 1998). Additionally, a recent study by Broadley *et al.* (2010) has led to the discovery of a *P. oculifer* specimen in Zimbabwe, where it is widespread and relatively common, usually found in low population densities. Similar to Namibia, this species is fairly common throughout Botswana yet little is known about its biology (Auerbach, 1987).

In Namibia, *P. oculifer* is concentrated mostly in the north-central regions of the country and avoids the dry western regions (Griffin, 2003). Published information on *P. oculifer* is limited with only one short study published on this species comparing its diet to its sympatric *S. pardalis* in central Namibia (Cunningham, 2006). *Stigmochelys pardalis* on the other hand, has been widely studied throughout southern Africa but very little research has been done on this species in Namibia.

The sympatric *S. pardalis* and *P. oculifer* have great variations in their physical characteristics and physiology. According to Boycott & Bourquin (2000), *S. pardalis* is southern Africa's largest tortoise species and is the fourth largest tortoise species in the world, achieving maximum carapace length of 700 mm. *Psammobates oculifer* species remains relatively small, with a shell length of 120-150 mm. It is considered to be an intermediate between a specialist and generalist feeder, and its diet includes a great variety of plants and fruits (Boycott & Bourquin, 2000). *Stigmochelys pardalis* on the other hand, is considered to be a generalized specialist, eating a broad range of plant species when stressed but generally specializing when preferred species are available after an increase in rainfall (Keswick, 2012).

Tortoises are ectotherms that rely on external heat to maintain their internal body temperatures. Their activity patterns are highly dependent on changes in external temperature and rainfall patterns. A study by Ragab & Prudhomme (2002) has estimated that by the year 2050, average annual temperatures are expected to increase by 1.5-2.5°C in southern Africa compared to the base period of 1961-1990. For ectothermic animals such as tortoises that are known to be evolutionary conservatives (they remain relatively

unchanged through time), Sinervo (2010) concludes that this rapid global temperature rise only provides them with two natural compensatory responses: 1. Given enough time and dispersal, species may either shift to more favorable thermal environments, or 2. They may adjust to new environments by behavioral and physiological adaptation. Alternatively, failure to adjust or adapt will result in demographic collapse and extinction.

Despite being ectotherms, McMaster & Downs (2013) state that tortoises, like all other reptiles have an ability to thermoregulate which is enhanced by adopting a variety of behavioural mechanisms. The use of retreat sites and selection of microhabitats are some of the different behavioural postures that enable reptiles to maintain their core body temperatures (T_b) above that of ambient temperatures (T_a) in winter or below the maximum T_a in summer (Sinervo, 2010). Similar to this study, Lambert (1981), Pulford *et al.* (1984), Wright *et al.* (1988), Hailey & Coulson (1996b) and Loehr, 2012) have all measured the T_b of tortoises; these temperatures were monitored in association with behavioural activity in the field.

In addition to thermoregulation, home range is an important aspect of every organism's niche and the two can be associated with each other. Grant & Dunham (1988) state that an organism's home range is a product of temporal changes in a reptile's thermal environment and the availability of suitable microclimates that may act as a constraint on its movement. Burt (1943) in simple terms defined home range as an area within which an animal can fulfill most of its basic life history requirements, such as shelter, foraging and reproduction. Geffen & Mendelsohn (1988) pointed out that tortoises are less vulnerable to predation than assumed but are more vulnerable to heat and drought in summer and cold in winter. Consequently, they may need to decentralize their home range around burrows or shelters during such periods, thereby restricting their habitat use.

The study aims to better understand the home range and thermal activity patterns of the sympatric *S. pardalis* and *P. oculifer*. Results from this study will seek to reduce the

current knowledge gap and provide critical baseline information for future studies on the Namibian tortoises, and importantly assist in future tortoise conservation efforts.

1.2 Objectives of the Study

- 1.2.1 To evaluate and compare activity patterns and behavior of sympatric *S. pardalis* and *P. oculifer* in relation to controlling habitat and environmental conditions (temperature, humidity, solar radiation and rainfall).
- 1.2.2 To evaluate and compare thermal refuge orientation of sympatric *S. pardalis* and *P. oculifer* in relation to diurnal and seasonal thermoregulation behavior.
- 1.2.3 To evaluate the home range and spatial overlap within and between *S. pardalis* and *P. oculifer*.

1.3 Hypotheses

- 1.3.1 H_0 : There is no significant difference between ambient, shell, iButton and surface temperatures of the tortoises.
 H_1 : There is a positive relationship between ambient, shell, iButton and surface temperatures of the tortoises.
- 1.3.2 H_0 : There is no significant difference in thermal refuge orientation and seasonality of tortoise exposure as a function of seasonal micro-climate conditions.
 H_1 : Tortoises thermal refuge orientation is mainly southerly during the wet season and northerly during the dry season.
- 1.3.3 H_0 : There is no difference between the home ranges of *S. pardalis* and *P. oculifer*.

H₁: *S. pardalis* is characterized by a larger average home range compared to *P. oculifer*.

1.3.4 H₀: There is no sample mean rear direction for either species and between seasons.

H₁: There is a sample mean rear direction for either species and between seasons.

1.4 Significance of the Study

According to Branch (1998), chelonians fossils date back to 210 million years ago. He further states that chelonians have not only survived the dinosaur era, but have also seen the explosive success of mammals, birds and man's sudden reign.

The opportunity to study the ecology of sympatric tortoise species is rare, nonetheless in one place in southern Africa, home to more than one third of the world's 45 tortoises. Due to its Africa-wide geographic distribution and large size, *S. pardalis* has been relatively well studied, however, its interaction and potential for competition with sympatric species is less understood. In the thorn-bush savanna near Windhoek, this species occurs sympatricly with the smaller *P. oculifer*.

Generally, information on habitat utilization, activity patterns and home range of Namibian tortoises is lacking with little ecological information available. As tortoises are poorly studied, scientific knowledge of their role in ecosystem functioning is patchy and incomplete. Although little is known about their role in maintaining and regulating ecosystem functions and, by extension, their potential value for supporting ecosystem services, tortoises are an abundant and diverse component of many terrestrial ecosystems contributing to a diverse range of ecological functions (Pough *et al.* 2004).

Published functions performed by tortoises in the ecosystems include, seed dispersal, nutrient re-distribution in faeces (Burney, *et al.*, 2013) and for deep burrowing species such as the Gopher tortoise (*Gopherus polyphemus*), extensive soil redistribution and underground habitat for commensal species (Stevenson, 2015). Tortoises also serve as a

source of food for birds, baboons and humans. A study by Fincham & Lambrechts (2014) observed that a pair of Pied Crows (*Corvus alba*) nesting on a windmill in the Ceres Karoo, South Africa rearing four chicks killed at least 160 in 2012 and 315 in 2013 small tortoises to feed the chicks and parents respectively. In remote tropical island ecosystems, tortoises take the role of keystone meso-herbivores and act as major ecosystem engineers (Griffiths & Zuel, 2013). Additionally, although to a lesser extent, tortoises can recycle micronutrients to the top soil layer in the process of digging and burrowing and may affect above ground vegetation community structure (Zug *et al.*, 2001).

A study by Gibbs *et al.* (2010) investigated the roles of the giant tortoises on the Galapagos Islands and found that these tortoises can indeed be referred to as ecological engineers. The impacts of tortoises on *Opuntia cactus* (Cactaceae) were evaluated in the Galapagos Islands, it is a keystone forage resource for many animals. The study showed that through browsing and trampling, tortoises strongly reduced the densities of small (0.5-1.5 m high) *O. cactus*, especially those near adulthood, and thereby reduced densities in larger size classes. Furthermore, tortoises also caused a shift from vegetative to sexual modes of reproduction in *O. cactus*. The study concluded that giant tortoises promote a sparse and scattered distribution in *O. cactus* and its associated biota in the Galapagos Islands. Gibbs *et al.* (2010) further stated that the effects of giant tortoises on terrestrial ecosystems of oceanic islands can equally be compared to those of mega-herbivores as drivers of savanna structure and function. Despite these studies, ecological roles of southern African (particularly Namibian) tortoises are poorly known and this leads to assumptions on the ecological roles and functions of these organisms in their respective ecosystems.

Sinervo (2010) has recently shown that tortoises are among many of the heliothermic species that are very sensitive to global warming and they may serve as indicator species in responding to rapid climate change.

The great tortoise diversity in Namibia, its sympatric species, the possibility of inter-specific competition and the importance of spatial separation are of great interest to both science and conservation. According to Cunningham & Simang (2006), it is generally

accepted that tortoise are the group of reptiles most under threat with numbers declining throughout Namibia as a result of competition with domestic stock, habitat destruction, road-kill, electric fences and consumption as food by humans and other predators. Despite this known fact, very little is known regarding tortoise ecology including basic aspects such as the home range and thermoregulation. Zug *et al.* (2001) stated that in order to set conservation priorities for these species, there is a need for a better understanding of the process of habitat selection, the integral roles of these species in their ecosystems, and anthropogenic influences on habitat selection and movement patterns. To develop conservation measures to protect land tortoises through a better understanding of population size and density, it is useful to know the size of their home ranges, amount of home-range overlap, and change of home range in different seasons (Geffen & Mendelssohn, 1988). Similarly to Keswick (2012), this study also attempts to understand what the tortoises do in the context of existing literature instead of how they do it. This study hopefully will be a valuable baseline study and contribute to future tortoise conservation measures in Namibia.

2. LITERATURE REVIEW

Namibia's arid lands are home to an array globally significant biodiversity, acclaimed for its species richness, habitat diversity and biological distinctiveness (UNDP, 2011). Namibia's diverse habitats possess a high level of endemism and according to Namibia's Fourth National Report to the United Nation Convention on Biological Diversity (2011), there is a total of 254 reptile species in Namibia of which 20% are considered endemic.

Many tortoises occupy harsh semi-arid habitats with high temperatures and very little rainfall and thus there is a need for them to employ a variety of tactics to cope with environmental fluxes. According to Meek (1984), the evolution of thermoregulatory behavior in chelonians almost certainly arose because environments are usually not thermally stable but fluctuate on a daily and seasonal basis. Different species will be affected by these environmental fluxes in different ways, including their size and reproductive status.

Thermoregulation in ectothermic reptiles is a combination of physiological and behavioral adaptations to maintain body temperature within an optimum range or to adjust physiology when the former is not possible (Huey, 1982). Behavioral thermoregulation takes the form of adjusting activity patterns to maximize or minimize heat uptake and avoid over-heating or chilling, through practices such as basking, seeking shade, aestivation or hibernation (Bradshaw, 1986). Active avoidance of heat has been recorded in many tortoises e.g. *Chelonoidis nigra* (McKay, 1964), *Gopherus spp.* (McGinnis & Voigt, 1971), *Dipsochelys dussumieri* (Frazier, 1973), and aestivation in *Gopherus* tortoises (Voigt & Johnson, 1976).

Very few aspects of tortoise ecology have been studied in southern Africa but those that have include amongst others, home range (Keswick, 2012; Hailey *et al.* 1996; McMaster & Downs, 2006, 2009), thermal activities (McMaster & Down, 2013), habitat selection (Cunningham, 2006; Cunningham *et al.* 2006), and phylogeography (Fritz *et al.* 2010).

A study on thermoregulation in *S. pardalis* by McMaster & Dawn (2013), radio-tracked 10 *S. pardalis* tortoises from 2002-2003; measured cloacal body temperatures and observed behaviours. To develop thermal profiles, core body temperatures were measured using Thermocron iButtons which were surgically implanted into the body cavities of 5 adult telemetered tortoises. The study highlighted that *S. pardalis* tortoises generally have unimodal activity patterns in winter (mid-day) and bimodal ones in summer (morning and afternoon). In winter, tortoises were active at lower body temperatures and at lower air temperature, when compared with summer. Tortoises maintained their core body temperature well below air temperature in summer and well above these in winter.

Tortoises are also heterotherms exhibiting wide fluctuations in body temperature (Stahl & Donoghue, 2010). They may respond to ambient temperature fluctuations by hiding in vegetation or undergoing periods of dormancy in vacant burrows (Highfield, 1990). Excessively low temperatures can cause decreases in metabolic rate, food intake and digestive performance, and excessively high temperatures can cause decreased food intake and weight loss (Stahl & Donoghue, 2010). This is in line with the findings of McMaster & Downs (2013).

Tortoises, like any other species, need food and water in order to survive. Depending on the environments, tortoises can either feed on what is readily available (generalize) or opt to eat only certain plant species from what is available (specialize). In Namibia, the unpredictable availability of water requires tortoises to develop physiological adaptations that will enable them to survive the long periods of drought when water and consequently forage are limited.

Stigmochelys pardalis can be found in most regions of Namibia except for the extreme arid western parts (Branch, 1998), this species is territorial and roams over large areas in search of food, water and potential mates (McMaster & Dawn, 2013). It is considered to be intermediate between a specialist and generalist feeder and its diet includes a great variety of plants and fruits (Boycott & Bourquin, 2000).

A study by Kabigumila (2001) observed feeding behaviour of *S. pardalis* in northern Tanzania and found that the natural diet was 97.8% plants (47 species from 213 families) most of which were succulent forbs, or non-woody flowering plants. In South Africa, Milton (1992), Rall and Fairall (1993), and Mason et al. (1999) observed the feeding behaviour of *S. pardalis* and concluded that grasses and bulbs were the principal components of the diet, but succulents were preferred. Fallen fruits, from marula (*Sclerocarya birrea*) were a food preference in some parts of southern Africa (Auerbach, 1987). Few studies have also shown that ingestion of bone and faeces can occur (Auerbach, 1987; Patterson, 1987; Highfield, 1990, 1996; Bonin, 2006). According to Boycott & Bourquin (1988), the ingestion of bones and faeces can be partially attributed to calcium and phosphorus requirements for shell growth and egg production.

Psammobates oculifer is endemic to southern Africa and occurs throughout the central and southern Kalahari regions (Branch, 1998). According to Griffin (2003), in Namibia this species avoids the dry western regions, and occurs throughout the central part of the country. The diet of this species is poorly known (Boycott & Bourquin, 2000), although Branch (1998) mentions that they prefer small succulents and grasses, as well as sheep and game droppings. However, Keswick (2012) stated that *P. oculifer* has a 'generalized specialist' diet, and it is able to eat a broad range of plant species when faced with drought but specializes when certain species become available after an increase in rainfall.

An important aspect in animal ecology is the concept of home range. It was initially proposed by Burt (1943), as a fundamental concept in spatial ecology. The home range of an animal is the area that encompasses all the resources the animal requires to survive and reproduce. McNab (1963) demonstrated that mammal home range size is a linear function of body size, and noted that carnivores have larger home ranges than similar sized herbivores. Tortoises are reported to have defined home ranges, but home-range sizes of some tortoise species are much larger than seems necessary to fulfill tortoises' biological requirements (Geffen & Mendelssohn, 1988). In addition, tortoises in arid areas generally have larger home ranges than those found in higher rainfall areas (Diemer, 1992). This suggests that home range may be determined by resource

availability (Geffen & Mendelsohn, 1988). In reptiles, home range sizes are generally associated with the distribution of one or more resources (e.g., food, shelter, mates, thermoregulation sites), and positive correlations between home range size and body size have been observed in many species. Sex, reproductive state, density, and food availability are some of the major factors that influence home range size in reptiles (Zug et al. 2001). Hailey & Coulson (1996) studied home range and daily movement distance of two African tortoises, Leopard tortoise (*S. pardalis*) and Speke's Hingeback Tortoise (*Kinixys spekii*) and found that *S. pardalis* exhibited proportionally larger home ranges than *K. spekii* and observed frequent movements by *G. pardalis* to an area with sodium-rich soils and argued that Leopard tortoises have exceptionally large home range because of the spatial distribution of sodium-rich soils rather than energetic requirements. The home range of the same organisms may also differ according to habitat type and quality (Diemer, 1992).

A study by Keswick (2012) found that on average *P. oculifer* males and females had home ranges of 5.36 ha and 23.0 ha respectively, whereas a study by McMaster & Down (2009) has shown that *S. pardalis* has home range of 5.70 ha on average and there was no significant difference between sexes but only between seasons. Both male and female *S. pardalis* had seasonally smallest home ranges during winter. Hailey & Coulson (1996) found that the short-term home range of *S. pardalis* was 26 ha in comparison to *K. spekii* that had a home range of 1.9 ha.

Gerlach (2005) concluded that virtually all tortoise species deliberately orient themselves relative to the sun position to either maximize warming (basking) or minimize overheating.

CHAPTER 3: RESEARCH DESIGN AND METHODOLOGY

3.1 Introduction

This study focuses on the temporal and spatial behaviour of *S. pardalis* and *P. oculifer* in the thorn-bush savannah of central Namibia. Field work was conducted between December 2013-April 2015 under a research and collecting permit (number 1851/2013) granted by the Ministry of Environment and Tourism (MET).

3.2 Study Area

This study was conducted at the Hohewarte Farm (S 22° 38'644" E 17° 24' 213) situated 45 km east of Windhoek (Figure 1). Hohewarte Farm covers an area of 10,400 ha and has an average annual rainfall of approximately 350-400 mm with most of the precipitation concentrated from January to April (Mendelsohn *et al.* 2002). Seasons were classified as follows: summer (October through March) and winter (April through September). The farm habitat is mixed shrub-land and thorn-bush savanna with dominant plant species such as *Ziziphus mucronata*, *Acacia hebaclada*, *A. karoo*, *A. erioloba*, *A. mellifera*, *Catophractus alexandrii*, and *Grewia* species, and *Eragrostis* and *Stipagrostis* grass species (Mendelsohn *et al.* 2002). Dry rivers, hills and mountains are other key habitats on Hohewarte Farm. The farm is home to both domestic livestock (cattle and horses) and native game species such as springbok (*Antidorcas marsupialis*), kudu (*Tragelaphus strepsiceros*), oryx (*Oryx gazella*), baboon (*Papio anubis*), warthog (*Phacochoerus africanus*), eland (*Tragelaphus oryx*), red hartebeest (*Alcelaphus buselaphus*), and many different bird species, amongst others. Southern Africa is one of the few places in the world where multiple sympatric tortoise species occur naturally (Juvik, personal communication). Two nearby but separate areas of the farm (Figure 2) with slight variation in physical characteristics were selected for intensive study. Analysis was based on pooled data from these sub-sites.

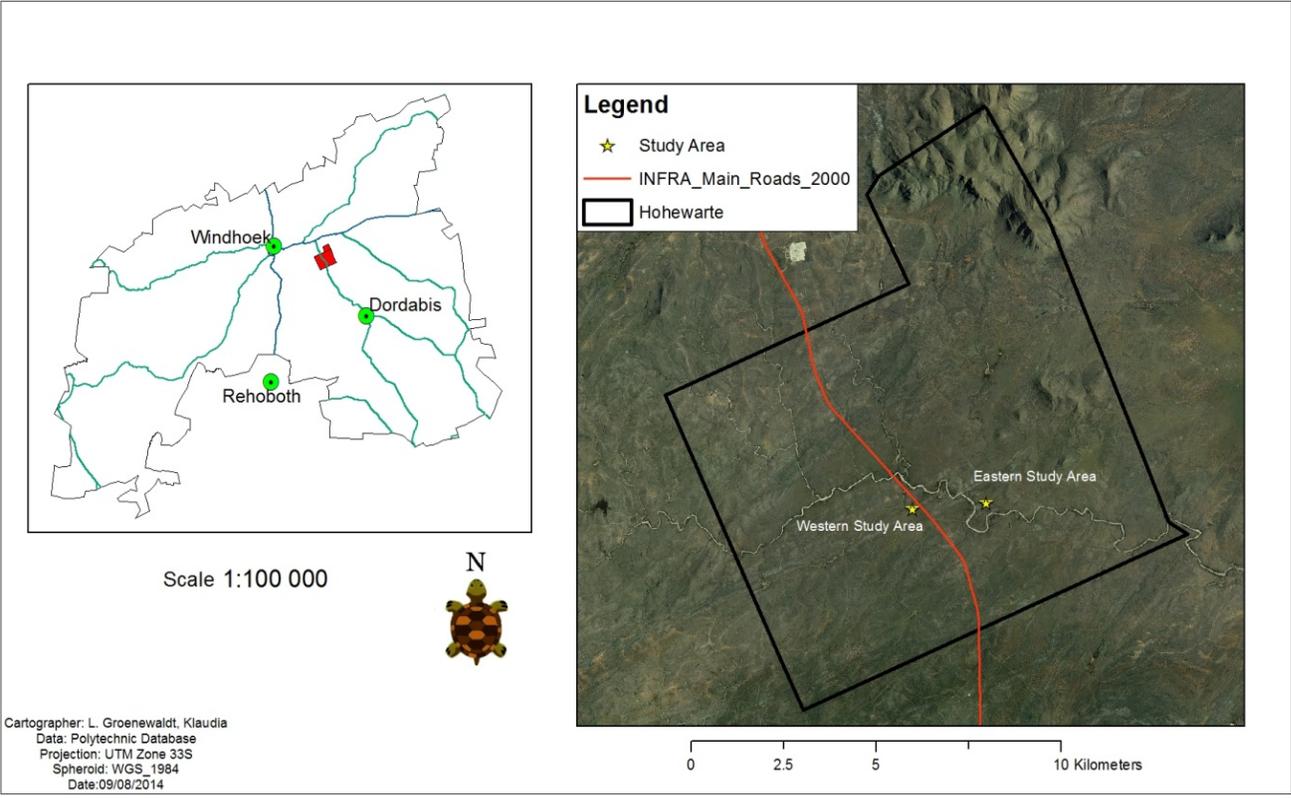


FIGURE 2: Location of the east and west field study sites at Hohewarte Farm. A tarred main road (INFRA Main Road) bisects the farm (map contributed by Lee Groenewaldt).

3.3 Monitoring movement and behavior of tortoise populations.

3.3.1 Radio Telemetry

Radio telemetry techniques have extensively revolutionized wildlife research (Mech, 2002) and many tortoise studies (Cunningham *et al.*, 2008; Frank *et al.*, 2011; Keswick, 2012; Wanchai, 2012) have utilized this technology.



FIGURE 3: Male *P. oculifer* tortoise with iButton and transmitter attached to its posterior end.

Thirty five (35) tortoises were fitted with a VHF transmitter (HoloHil or Namtrack models) and temperature logger to the lower posterior end (male) and lower anterior end (female) of the carapace using clear epoxy glue (long lasting but harmless to the animal). According to Barrett (1990), anterior placement of transmitters and iButtons in females is to avoid interference with mating. Each transmitter had a unique frequency which allowed for subsequent independent tracking and recapture of individuals.

The attached HoloHil transmitter weighed 6 g and 13 g for juveniles and adults respectively (the smallest transmitter weighed 1.8 g). NamTrack transmitters weighed 8 g

and 11 g for juveniles and adults respectively; both models did not exceed the recommended attachment weight guidelines of 12% of body weight (Keswick, 2012). Most transmitters' life spans ranged between 6-25 months (depending on the manufacturer) with an exception of the smallest transmitter lasting for 27 days only. Tortoise locations were monitored using an R-1000 Telemetry Solutions receiver and hand-held Yagi antenna. The study was based on a total of 35 telemetered tortoises. However, by the end of the study, only 24 tortoises (14 *S. pardalis* and 10 *P. oculifer*) were tracked. Nine (9) *S. pardalis* and 1 *P. oculifer* tortoises disappeared without any trace; 1 *S. pardalis* tortoise lost its front leg during an attack by a baboon and 1 *P. oculifer* tortoise died by drowning in a burrow. Of the remaining 24 tortoises, 8 were females (6 *S. pardalis* and 2 *P. oculifer*); 10 males (3 *S. pardalis* and 7 *P. oculifer*) and 6 juveniles (5 *S. pardalis* and 1 *P. oculifer*). All tortoises monitored in this study were captured at weekly or bi-weekly intervals. A total of 62 days (496 hours) were spent in the field.

3.3.2 Thermal activities and refuge “lay-up” characteristics.

To determine daily temperature variations, telemetered tortoises were equipped with carapace mounted temperature loggers (iButtons) that record temperature at 12 minute intervals. Data was downloaded 2-3 times a week from the loggers using Thermodata 3 software. In addition to the continuously logged temperature data, the following specific information were recorded immediately after tortoises were periodically recaptured in the field: solar radiation (w/m^2) using the solar power meter, exposed ground-surface temperature ($^{\circ}\text{C}$), laid-up (ground on which the tortoise was resting) surface temperature ($^{\circ}\text{C}$), front and rear leg; and shell temperature ($^{\circ}\text{C}$) using the Raytek-Raynger ST temperature gun. Additional information recorded included time of day; sky (sunny, partly cloudy, mostly cloudy) and atmospheric (rain, drizzle, windy) conditions; tortoise rear orientation relative to the sun; percentage of the tortoise carapace shaded; grade position (was the tortoise below or above the ground level) (Hohewarte field data sheet, Appendix 1).

Table 1: Description of *S. pardalis* and *P. oculifer* common behaviours as recorded at Hohewarte Farm, December 2013 to April 2015.

	Behaviour	Description
Active	Feeding	Biting any food item.
	Walking	Locomotion of any form.
Inactive	Resting	Under vegetation in shade with both head, front and rear legs in carapace.
	Basking	Motionless in the open with legs and head extended outside of the carapace; and part or all of the carapace is exposed to the sun.

A meteorological station was deployed on site to continuously record ambient temperature, humidity, solar radiation and rainfall. Ambient temperature was recorded at 20 cm above ground level. Four copper tortoise models were placed a few meters from the meteorological station with separate temperature data loggers within each tortoise model. The tortoise models varied in size; the smaller sized tortoise models represented *P. oculifer* whereas the larger sized tortoise models represented *S. pardalis*. Two smaller copper models were placed under the shade; 1 large and 1 small copper model in the full sun.

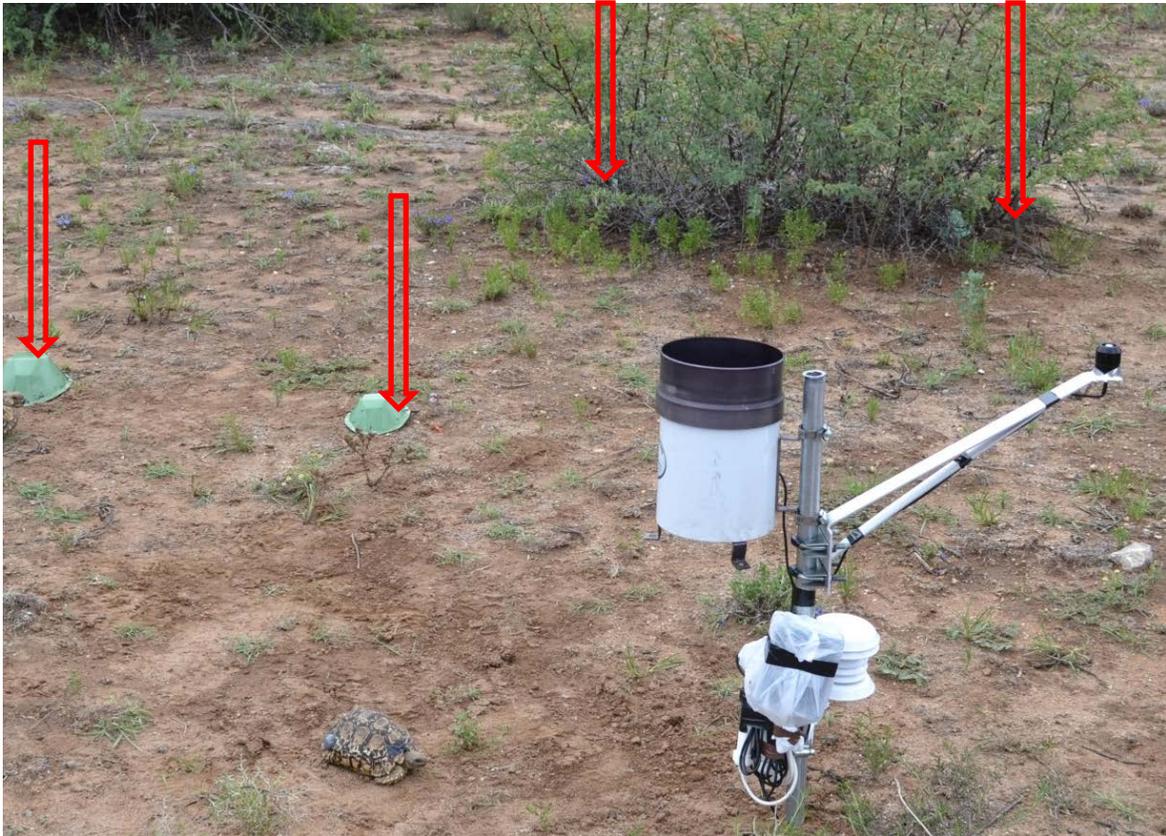


FIGURE 4: Meteorological station deployed at the study site. Variables measured included soil moisture, solar radiation, rainfall and humidity. Copper tortoise models (red arrows) were also placed close to the meteorological station, two under the shade and two were placed in the open.

If a tortoise was found in a refuge, the orientation of the rear end of the tortoise relative to the sun was recorded using an MC-2 Suunto compass, and obvious landmarks (e.g Rosenberg Mountain) located in directions known to observers. The extent to which a tortoise was covered by vegetation in its shelter was categorized as broad percentages in 4 groups: 0%–24%, 25%–49%, 50%–74%, or 75%–100% cover. Additionally, information such as location, topography, habitat, vegetation type at each shelter, as well as the percentage of the tortoise covered by shade and its orientation, were recorded.

All tortoises were sexed (male, female or juvenile), weighed (g) using a portable electronic weighing scale or a hang scale, and body measurements were recorded using Vernier calipers (plastron length—gular notch to anal notch) in the field.

3.3.3 Home Range

Tortoise recapture geographic coordinates were recorded with a hand-held Garmin (eTrex model) Global Positioning System (GPS) instrument using the World Geographic System (WGS) 84 datum for southern Africa, expressed in latitude and longitude. Cumulative locational data for each tortoise were converted to 100% Minimum Convex Polygon (MCP).

3.4 Data Analyses

A Shapiro-Wilk's test for normality indicated that the values of annual home range areas (MCP) and mean distances moved between locations were non-normally distributed. All other data were also not normally distributed.

The extent of the annual and seasonal home range sizes were delineated in ESRI's ArcGIS 10.2 statistical software. To determine if there was any significant difference between the home range size between species and season, a two-way ANOVA statistical test in Excel was used. 95% Kernel Density (KD) in ArcGIS 10.2 was used to display any evident home range overlaps between the species. Kernel Density estimation was also used to delineate the core activity areas within the home range.

To determine whether the differences between the different temperature variables was significant, a two way-ANOVA test in Excel was used to calculate this difference. Simple regression (r^2) analysis was done in order to describe the relationship between the different temperature variables associated with the two tortoise species and determine which temperature variable can be used to best describe the body temperatures of each. Prior to the regression analysis, data was transformed using \log_{10} transformation for normal distribution.

Orientation data was analyzed using Microsoft Excel. The Rayleigh z test (Zar, 1981) was used to test the null hypothesis that there is no sample mean rear direction. The Rayleigh z statistic value was determined using the equation: $z=nr^2$, where n is the sample size and r is taken from the mean angle equation. Chi-square statistical test in Microsoft Excel was used to determine if there is any significant difference.

4. RESULTS

This chapter presents results on the home range, thermal profiles and orientation of the sympatric *P. oculifer* and *S. pardalis*.

4.1 Home Range

The seasonal and annual home range data obtained for both *P. oculifer* and *S. pardalis* were not normally distributed ($W = 0.724$, $df = 8$; $p = 0.011$).

TABLE 2: Average home range sizes (ha) of male, female and juvenile *S. pardalis* and *P. oculifer* during the wet season, dry season and throughout the study period.

Species	ID	Sex	Size (g)	Records	Average Seasonal Home Range size (ha)		
					Wet	Dry	Annual
<i>S. pardalis</i>	Stpa2	F	6894	56	16.7	16.8	34.00
	Stpa5	F	909	41	2.9	1.5	5.00
	Stpa11	F	8397	28	34.4	1.7	42.00
	Stpa15	F	6346	26	1.7	3.0	9.00
	Stpa19	F	1002	13	0.7	-*	1.00
	Stpa17	M	2698	22	83.6	0.8	58.00
	Stpa14	J	438	43	13.6	2.3	9.81
	Stpa20	J	364	13	0.3	-*	1.00
<i>P. oculifer</i>	Psoc1	M	319	51	4.5	0.3	10.00
	Psoc2	M	339	51	13.6	5.4	35.00
	Psoc3	M	272	41	9.2	2.3	55.00
	Psoc5	M	349	58	151.4	5.3	299.00
	Psoc7	M	235	47	16.0	7.0	101.00
	Psoc9	M	254	27	6.9	0.4	11.00
	Psoc8	F	483	34	3.3	0.4	5.00
	Psoc6	F	321	52	2.0	2.1	5.00

* No data was recorded

Male *P. oculifer* No. 5 (highlighted red in Table 2) had the largest annual home range size of 299.0 ha. This value is considered an outlier that will affect the average home range size of *P. oculifer* and the comparisons between the species will be biased towards *P. oculifer*.

Female *S. pardalis* had smaller home range sizes compared to the male *S. pardalis* (Table 1). Regardless of sex, larger *S. pardalis* had larger home range sizes (Stpa2, Stpa11 and Stpa17) followed by the medium sized *S. pardalis* (Stpa5 and Stpa19). The smaller *S. pardalis* had the smallest home range sizes (Stpa 20). Like its sympatric species, *P. oculifer* had the same observed trend. Overall, male *P. oculifer* had larger home range sizes compared to the female *P. oculifer* (Table 1). Between species, the smaller sized *P. oculifer* had the larger home range sizes compared to the larger *S. pardalis*.

4.1.1 Annual Home Range

There was no significant difference in the annual home range size of *P. oculifer* and *S. pardalis* $P(0.39) > 0.05$, $df=7$.

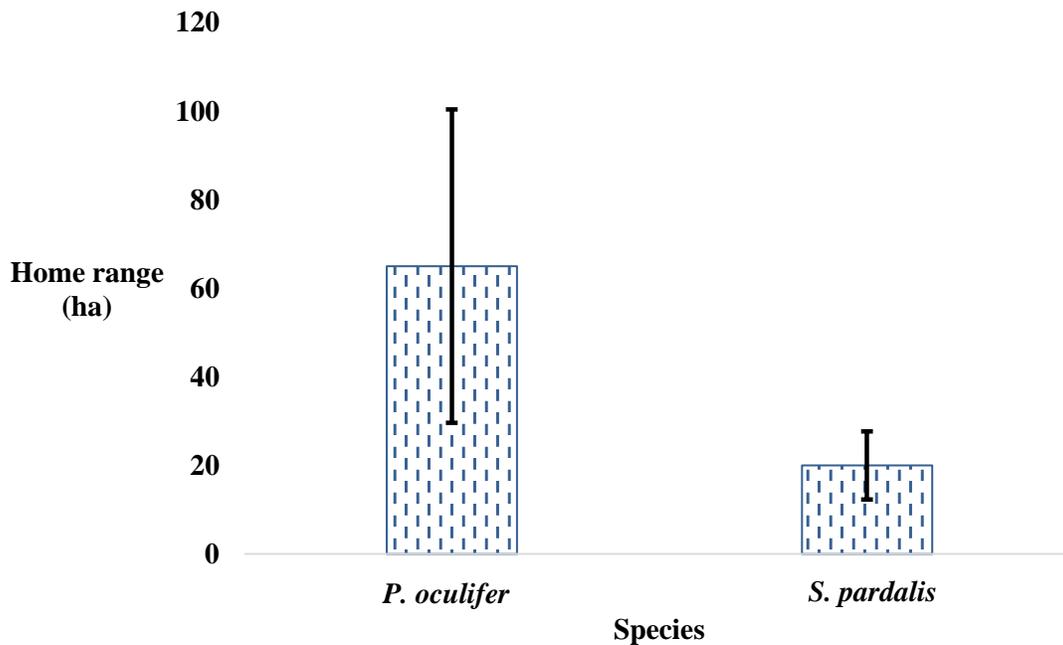


FIGURE 5: A comparison of the overall average annual home range size for *P. oculifer* and *S. pardalis* at Hohewarte Farm.

On average, *P. oculifer* had the largest annual home range (64 ha) (range 5-299ha) compared to *S. pardalis* (20 ha) (range 1-58ha). These home range sizes are irrespective of size and sex within the species.

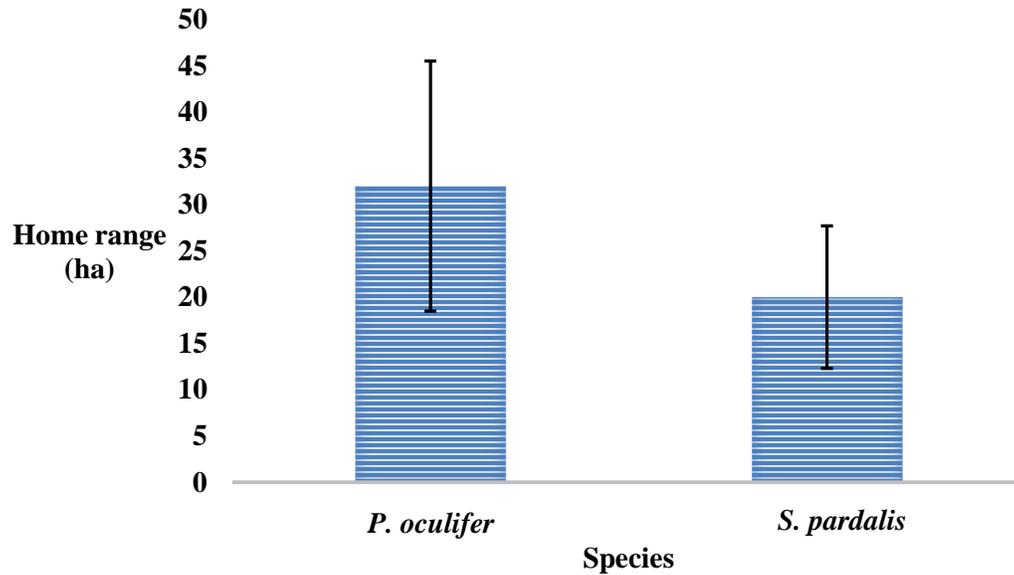


FIGURE 6: A comparison of the overall average annual home range size for *P. oculifer* (excluding Psoc 5) and *S. pardalis* at Hohewarte Farm.

When Psoc 5 is excluded, the average annual home range for *P. oculifer* is reduced to 32 ha (compared to 64 ha when Psoc 5 is included in the analysis). Results indicate that the annual home range of *P. oculifer* (without outliers) is still larger than the annual home range of *S. pardalis*.

4.1.2 Seasonal Home Ranges

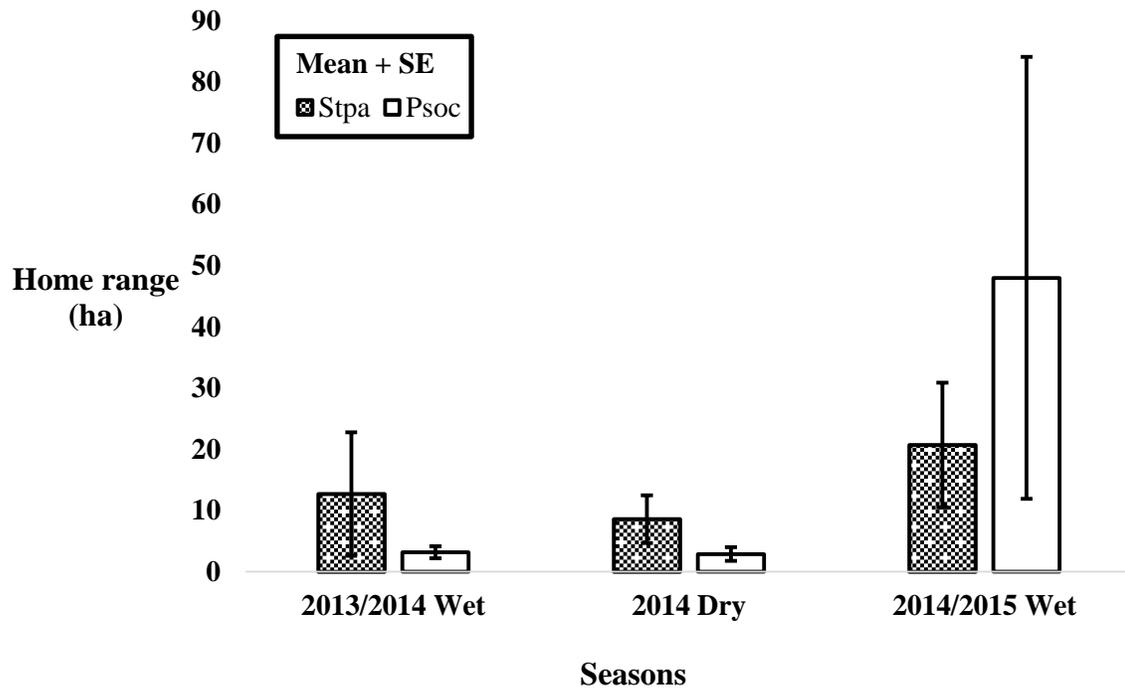


FIGURE 7: Seasonal home range size (ha) of *S. pardalis* and *P. oculifer* from December 2013 to April 2015.

P. oculifer had its largest average home range (48 ha) during the 2014/2015 wet season compared to its sympatric *S. pardalis*. *S. pardalis* had its largest home range during the 2014 dry season and the 2013/2014 wet season.

4.1.3 Home Range Overlap

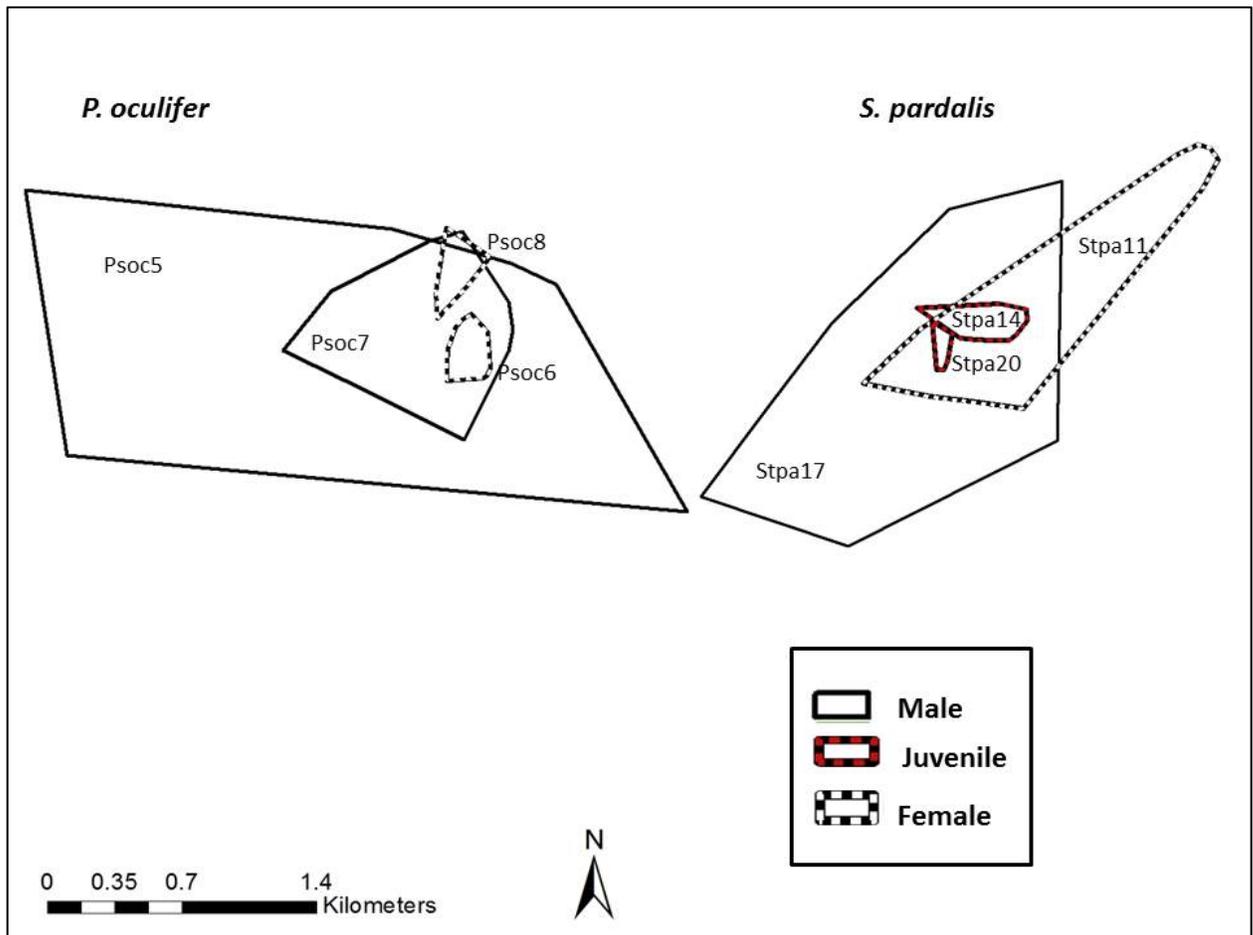


FIGURE 8: A comparison of the annual home range overlap (100% MCPs) for (a) two male and female *P. oculifer*, and (b) two juveniles; and one male and female *S. pardalis* at Hohewarte Farm.

Male tortoises (Psoc5 and Stpa17) had larger annual home ranges compared to the female tortoises (Psoc6, Psoc8 and Stpa11) for both species. The juvenile tortoises (Stpa14 and Stpa20; sex unknown) had the smallest home range sizes for both species.

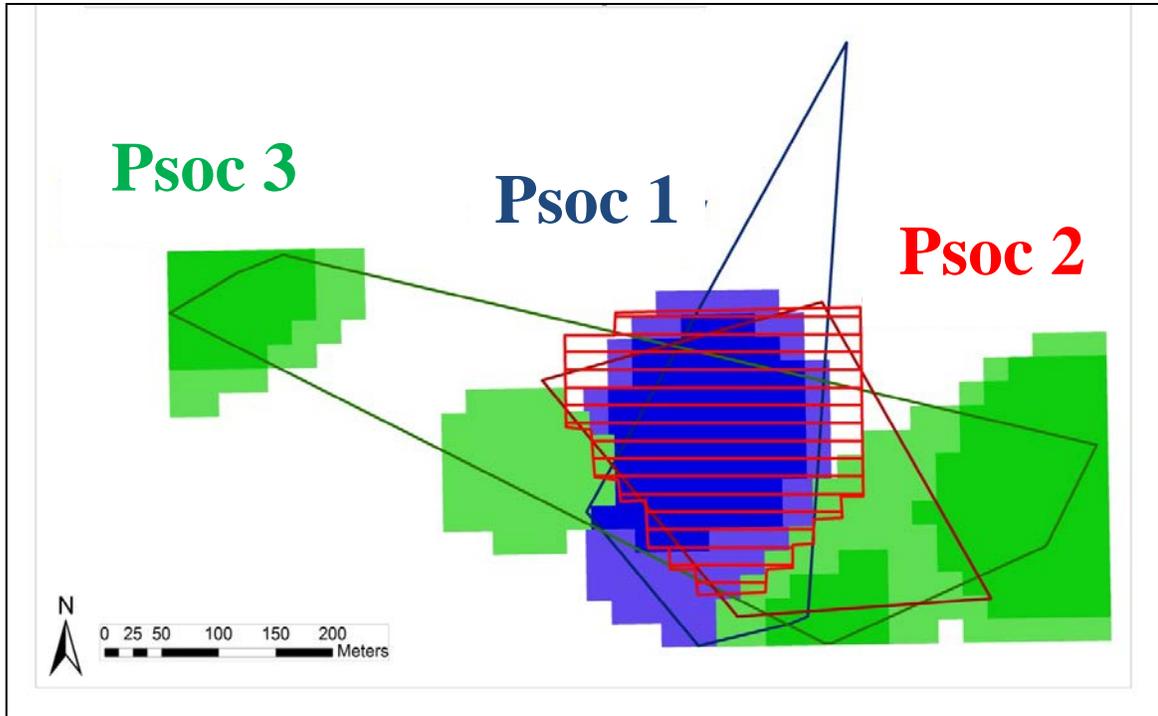


FIGURE 9: Illustrations displaying home range overlap (100% MCPs) between three (3) male *P. oculifer*. Green = Psoc 3; Blue = Psoc 1 and Red = Psoc 2.

The home ranges of three (3) male *P. oculifer* tortoises evidently overlapped with one another in the centre of all the 3 home ranges. The core activity areas for all tortoises were however different, Psoc 3 had core areas outside the area of overlap while the core activity areas of Psoc 1 and Psoc 2 coincided with the area of overlap.

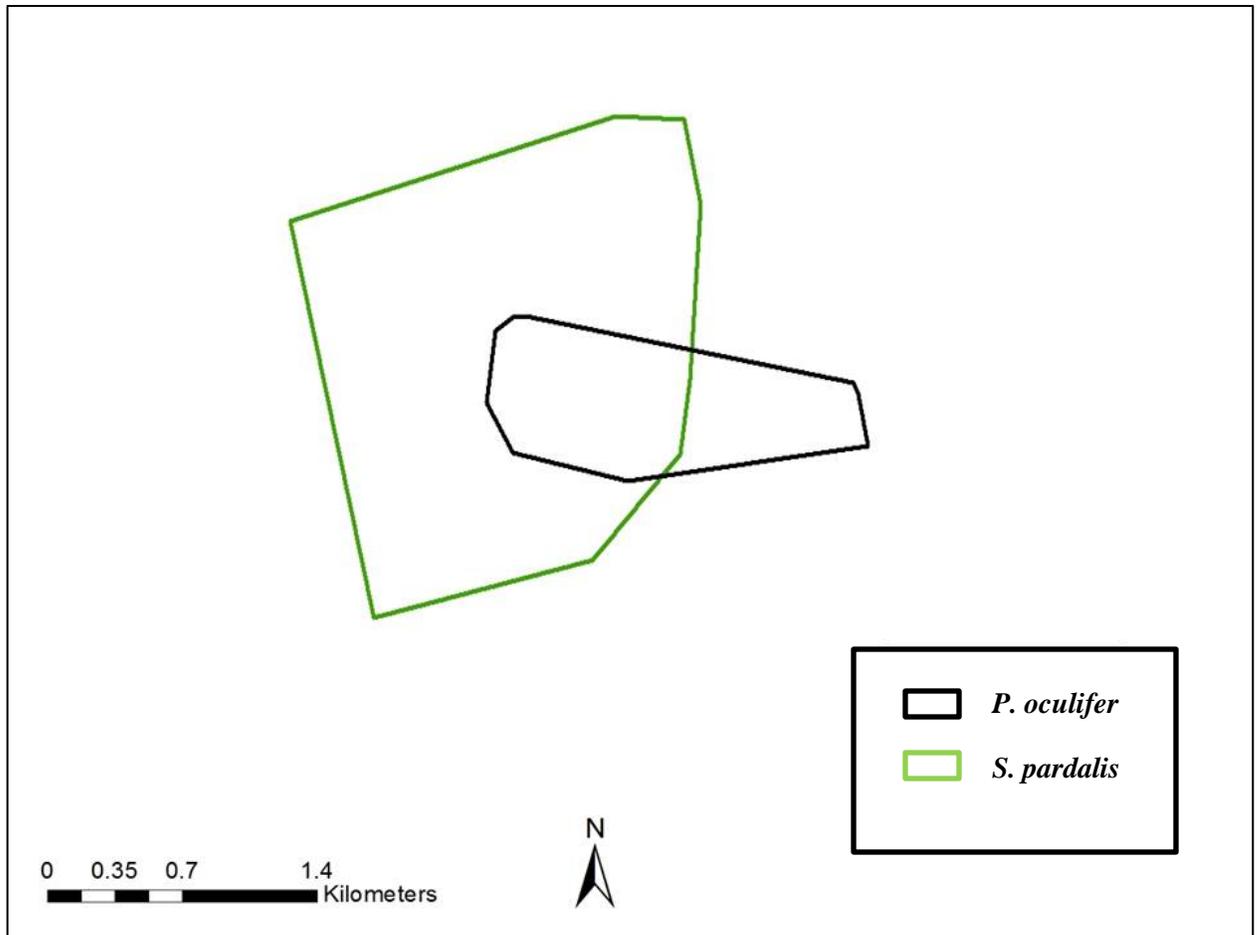


FIGURE 10: A comparison of the annual home range overlap (100% MCPs) and size for *P. oculifer* and *S. pardalis* at Hohewarte Farm.

Species home range overlap was evident between several individual *P. oculifer* and *S. pardalis* tortoises. Home range overlap was observed regardless of sex and size.

4.2 Temperature

Temperature data associated with the tortoises and meteorological station were also not normally distributed ($W = 0.938$, $df = 36$; $p = 0.045$).

There was no significant difference between the different temperature variables associated with the individual *P. oculifer* tortoise (Psoc#1) (two-way ANOVA, $P < 0.0012$) per season. The wet season temperatures did not significantly differ from the dry seasons although it was found that temperatures recorded during the wet season were much higher than those recorded during the dry seasons. On Average, the highest temperature recorded for the wet seasons was 48.5°C (copper model) while the lowest was 31.1°C (shell). The lowest recorded average temperature was 24.9°C (iButton) in the dry season and 33.8°C (copper model) was the highest recorded temperature.

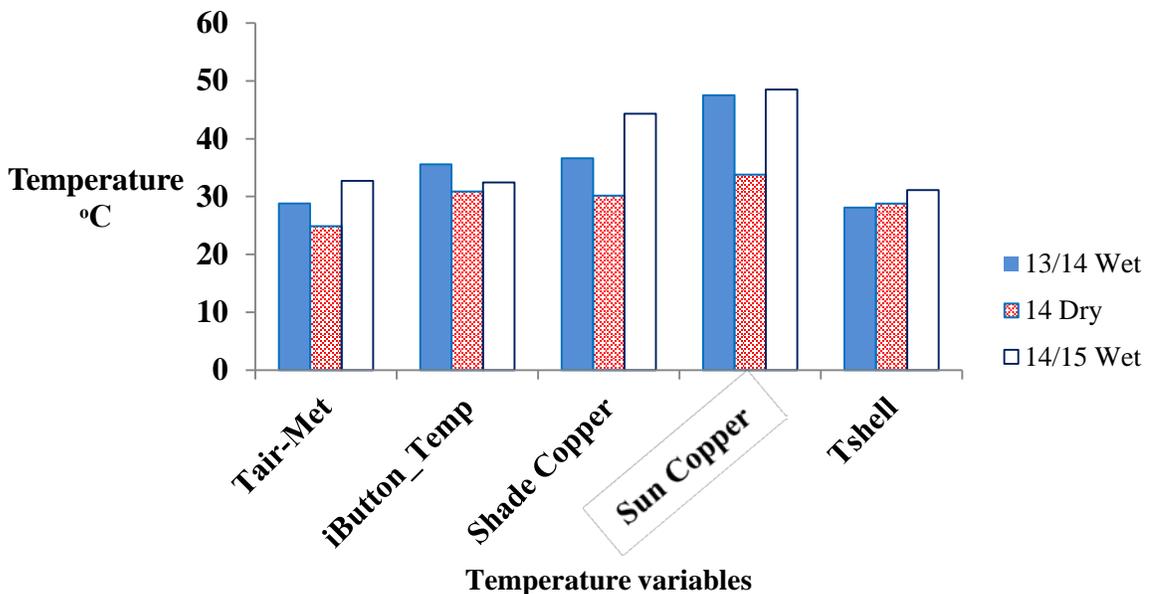


FIGURE 11: Thermal comparisons between the tortoise shell, iButton, copper model in the sun, copper model in the shade and the ambient temperature from the weather station for *P. oculifer* during the wet and dry seasons of 2014/2015. Tair-Met=air temperature recorded at the meteorological station; iButton_Temp=temperature recorded by the iButton; Shade Copper=temperature recorded by the copper tortoise in the shade; Sun Copper=temperature recorded by the copper tortoise in the sun; Tshell=temperature recorded on the tortoise shells.

For *P. oculifer*, associated temperatures were higher during the wet seasons and were the lowest during the dry seasons. The 2014 dry season had the lowest temperatures recorded during the study period while the 2014/2015 wet season had the highest temperatures recorded. The copper tortoise model in the sun had the highest recorded temperatures in all seasons during the study period while the meteorological station had the least.

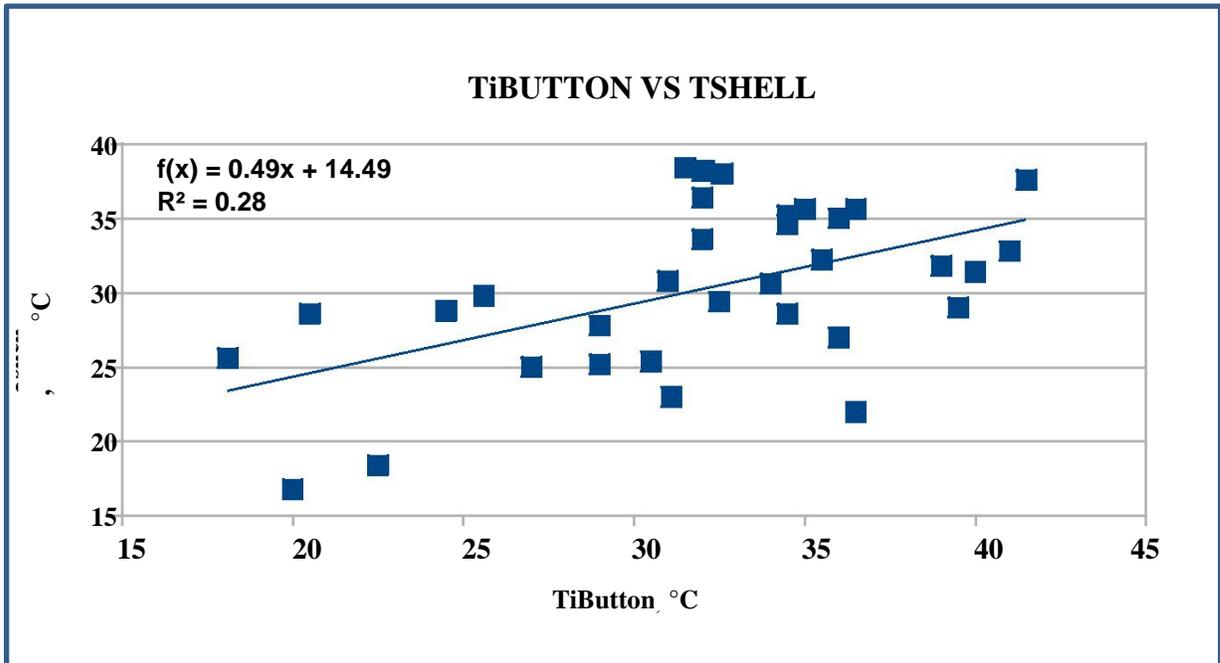


FIGURE 12: Linear regression analysis of the iButton and shell temperatures for *P. oculifer* at Hohewarte Farm. TiButton=iButton temperature; Tshell=shell temperature. (Assisted by Michealene Iaukea-Lum).

The regression analysis indicates that the shell temperature increased with an increase in the temperature recorded by the iButton. Although the two variables are not directly dependent upon each other, their readings are both influenced by the ambient temperature. Results show that there is a weak relationship ($R^2 = 0.28$) between the two variables.

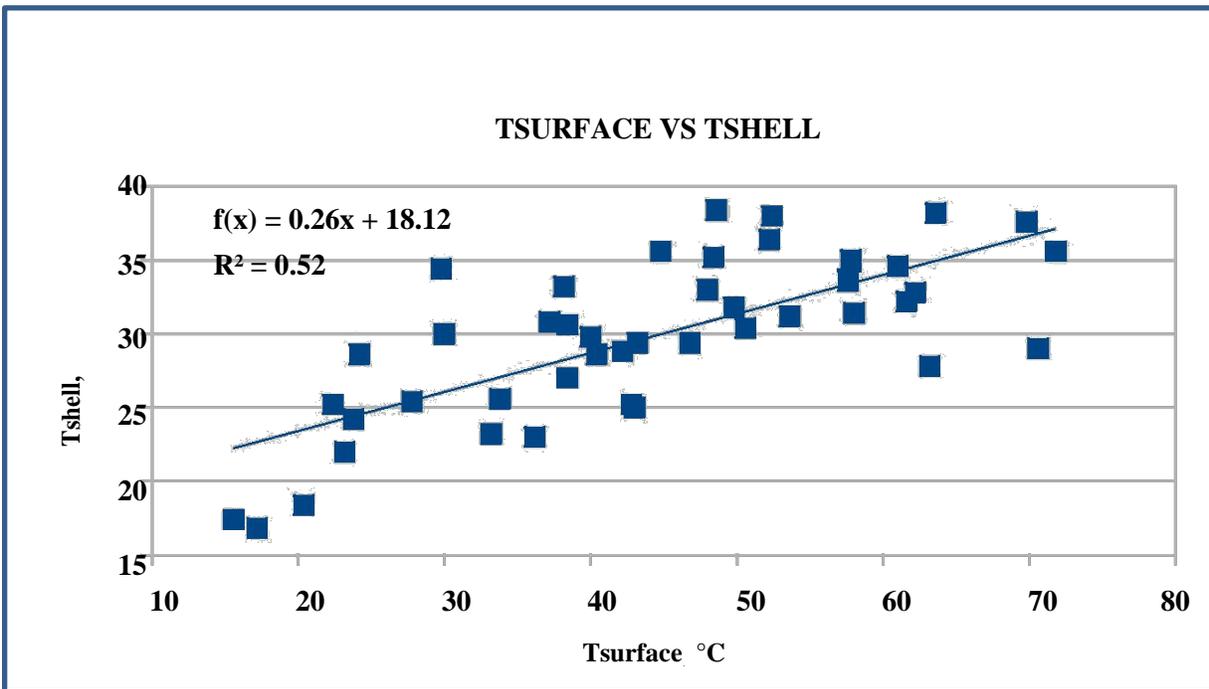


FIGURE 13: Regression analysis between the surface and the shell temperatures for *P. oculifer*. Tsurface=surface temperature; Tshell=shell temperature (assisted by Michealene Iaukea-Lum).

The regression analysis indicates that the shell temperature increases with an increase in the surface temperature recorded during tortoise recaptures. Results show that there is a slightly strong relationship ($R^2 = 0.52$) between the two variables.

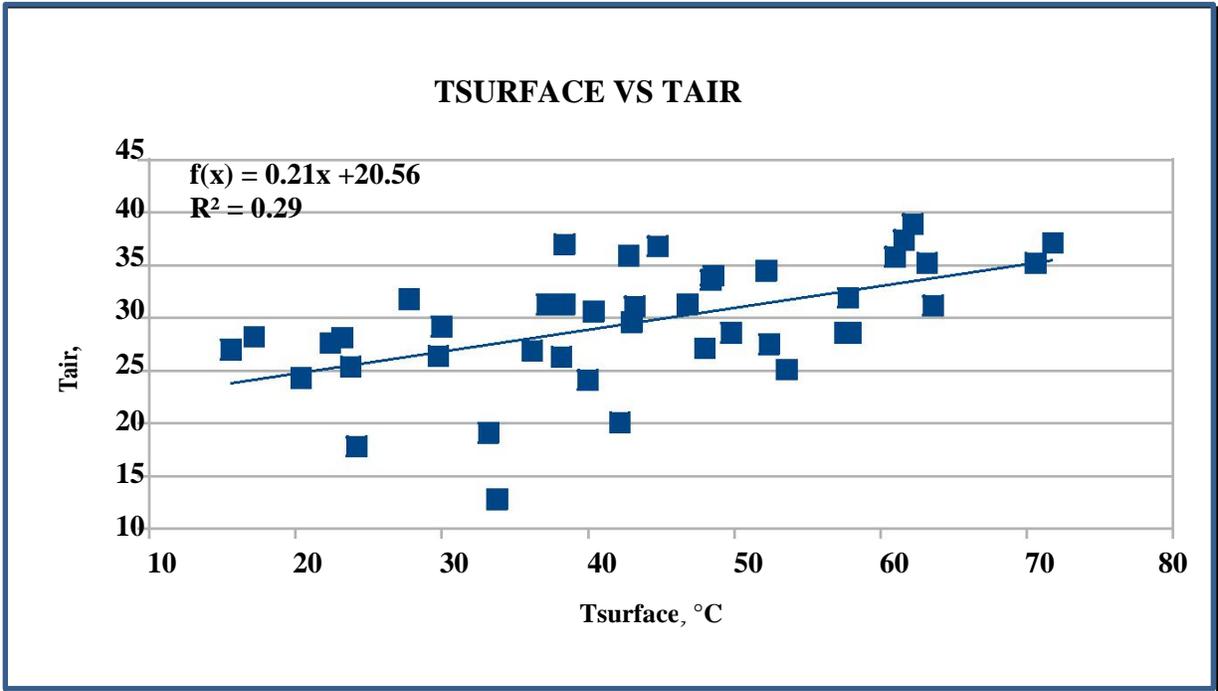


FIGURE 14: Linear regression analysis between the surface and air (recorded by the meteorological station) temperatures for *P. oculifer*. Tsurface= surface temperature; Tair=air temperature (assisted by Michealene Iaukea-Lum).

The regression analysis indicates that there is a positive relationship between the air temperature and the surface temperature. The two variables are directly dependent upon each other, i.e the surface temperature is influenced by the ambient temperature. Results show that there is a weak relationship ($R^2 = 0.29$) between the two variables.

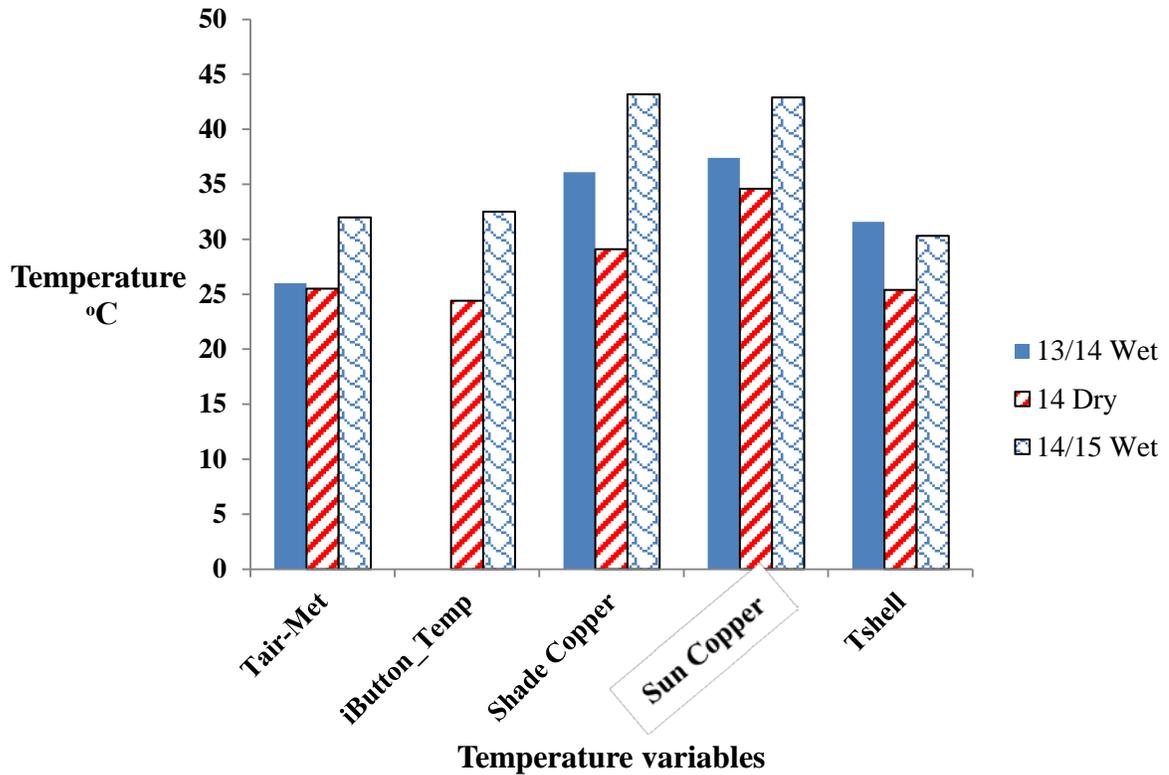


FIGURE 15: Thermal comparisons between the tortoise shell, iButton, copper model in the sun, copper model in the shade and the ambient temperature from the weather station for *S. pardalis* during the wet and dry seasons of 2014 and 2015. Tair_Met=air temperature recorded at the meteorological station; iButton_Temp=temperature recorded by the iButton; Shade Copper=temperature recorded by the copper tortoise in the shade; Sun Copper=temperature recorded by the copper tortoise in the sun; Tshell=temperature recorded on the tortoise shells.

For *S. pardalis*, associated temperatures were also higher during the wet seasons and were the lowest during the dry season. The 2014 dry season had the lowest temperatures recorded during the study period while the 2014/2015 wet season had the highest temperatures recorded. The copper tortoise model in the sun had the highest recorded temperatures in all seasons during the study period while the iButton had the least.

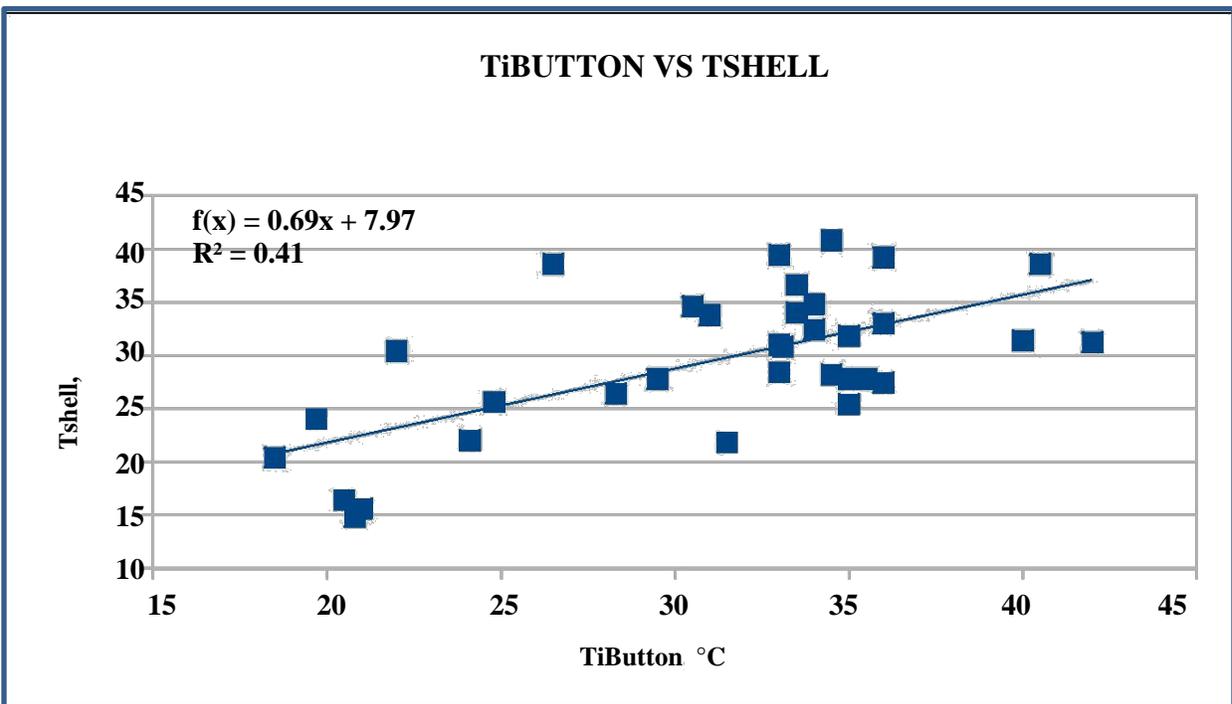


FIGURE 16: Regression analysis between the iButton and shell temperatures for *S. pardalis*. TiButton=iButton temperature; Tshell=shell temperature (assisted by Michealene Iaukea-Lum).

The regression analysis indicates that the shell temperature increases with an increase in the temperature recorded by the iButton. Although the two variables are not directly dependent upon each other, their readings are both influenced by the ambient temperature. Results show that there is a weak relationship ($R^2 = 0.41$) between the two variables.

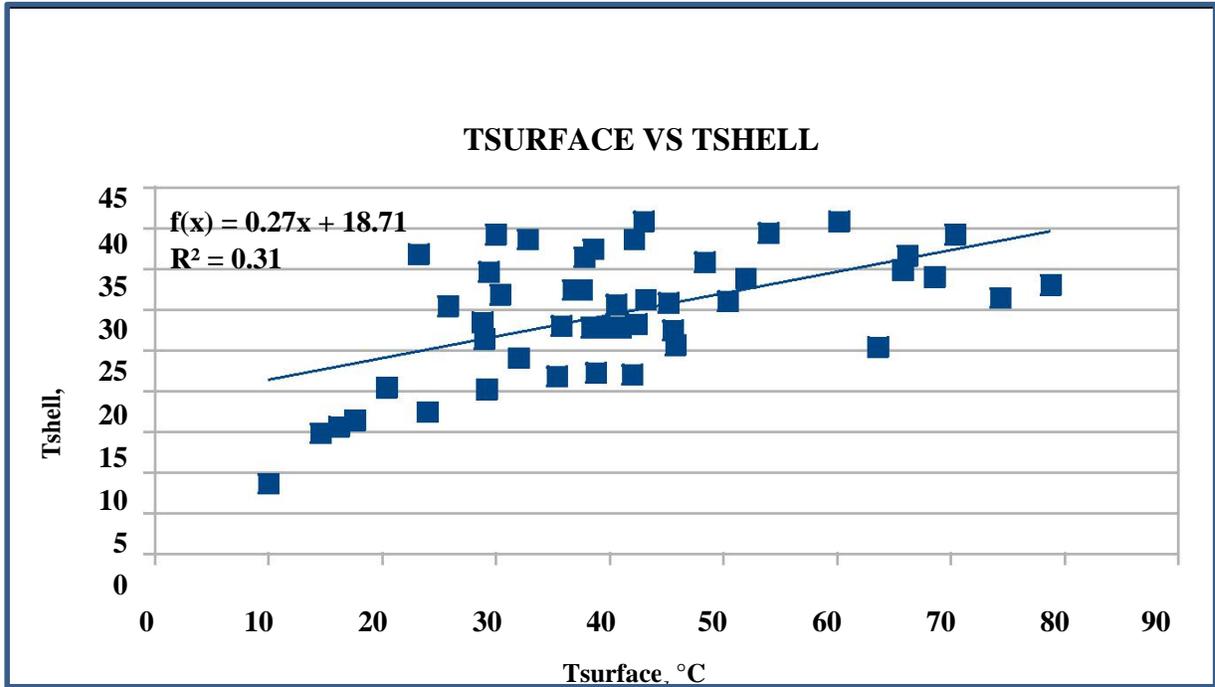


FIGURE 17: Regression analysis between the surface and the shell temperatures for *S. pardalis*. Tsurface=surface temperature; Tshell=shell temperature (assisted by Michealene Iaukea-Lum).

The regression analysis indicates that the shell temperature increases with an increase in the surface temperature recorded during tortoise recaptures. Results show that there is a weak relationship ($R^2 = 0.31$) between the two variables.

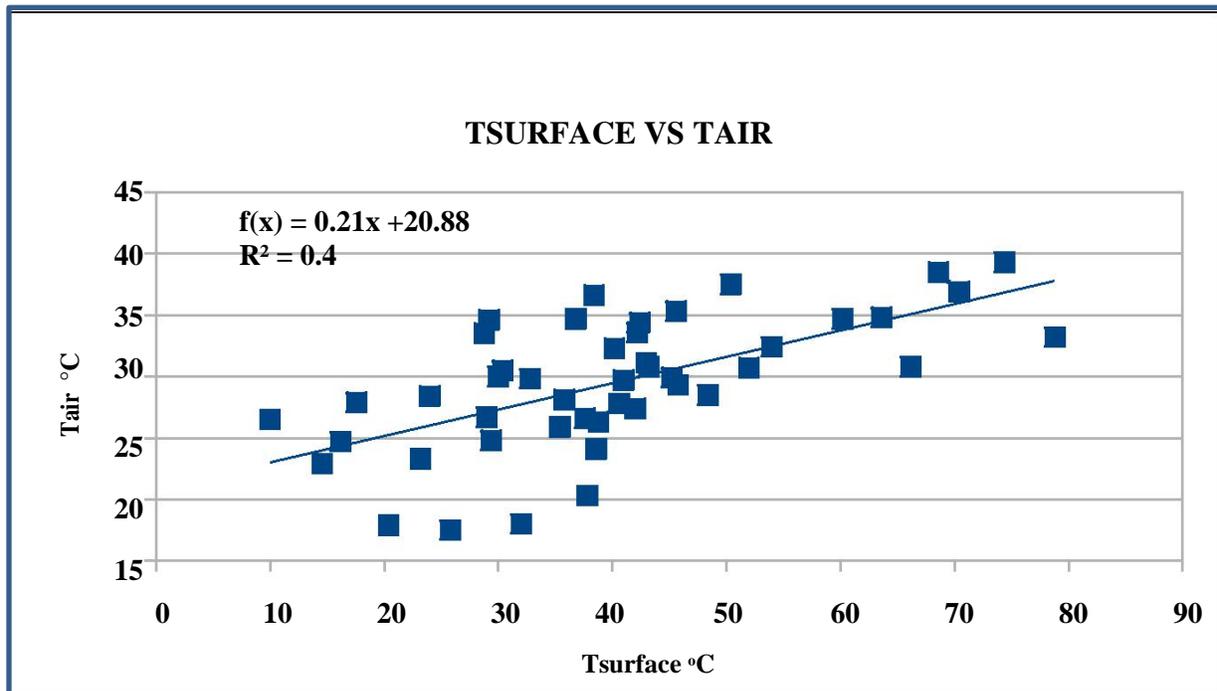


FIGURE 18: Regression analysis between the surface and the air (recorded by the meteorological station) temperatures for *S. pardalis*. Tsurface=surface temperature; Tair=air temperature (assisted by Michealene Iaukea-Lum).

The regression analysis indicates that there is a positive relationship between the air temperature and the surface temperature. Although the two variables are directly dependent upon each other, i.e the surface temperature is influenced by the ambient temperature. Results show that there is a weak relationship ($R^2 = 0.40$) between the two variables.

4.3 Orientation

Results from Rayleigh's Z statistical test (Rayleigh $Z=7.075$, $P < 0.001$) indicated that there was no mean direction for the species orientation. There was also no observed significant difference (X^2 , $P > 0.030$) between orientation directions of the species and seasons.

The mean rear shell orientation throughout the seasons was NE for both species. The rear orientation directions was not uniform but rather random.

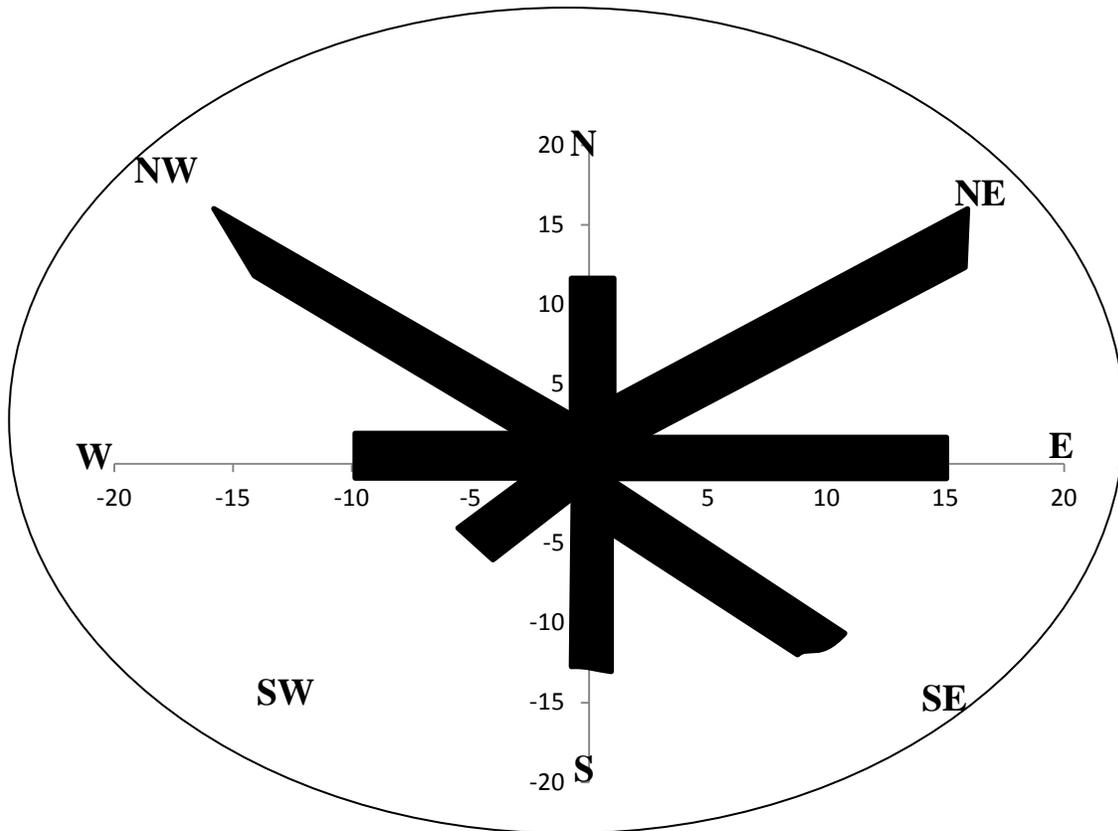


FIGURE 19: Illustration of the average rear orientation (%) of *S. pardalis* during the dry season.

The overall rear orientation for *S. pardalis* during the dry seasons was predominantly in the north westerly and easterly directions.

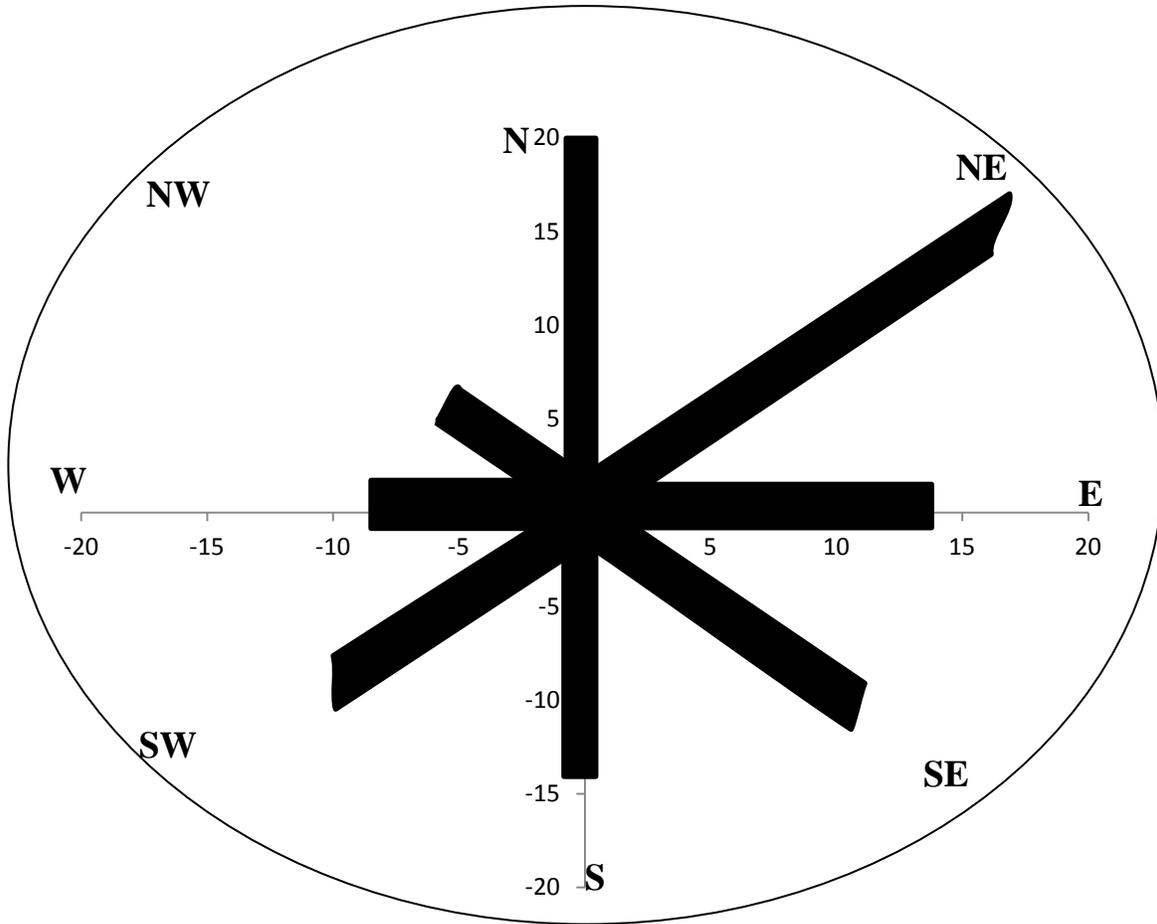


FIGURE 20: Illustration of the average rear orientation (%) of *S. pardalis* during the wet season.

The overall rear orientation for *S. pardalis* during the wet seasons was predominantly in the southerly, easterly and northerly directions.

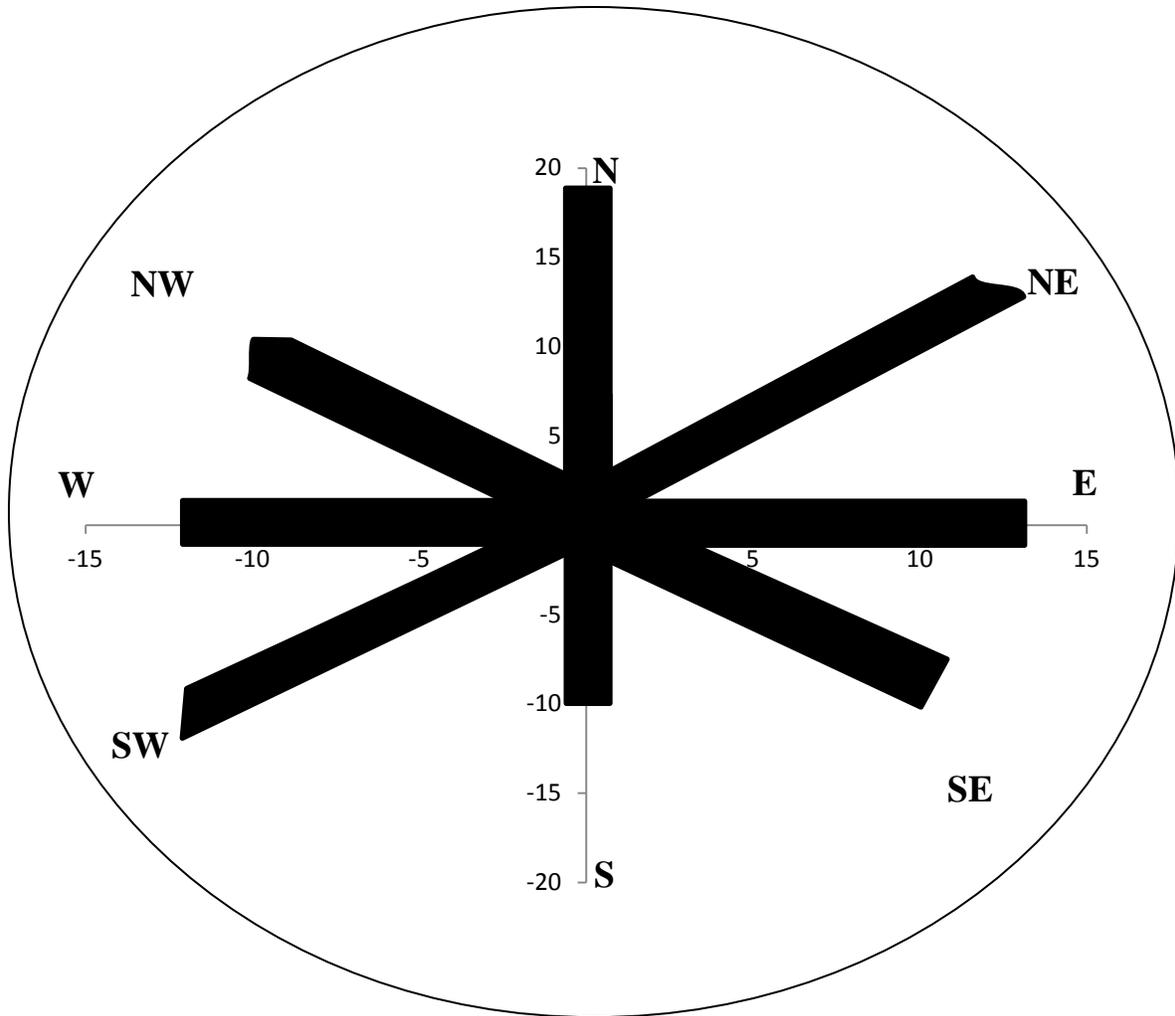


FIGURE 21: Illustration of the average rear orientation (%) of *P. oculifer* during the dry season.

The overall rear orientation for *P. oculifer* during the dry seasons was predominantly in the northerly, easterly and westerly directions. The species seem to have avoided the southern direction during the dry season.

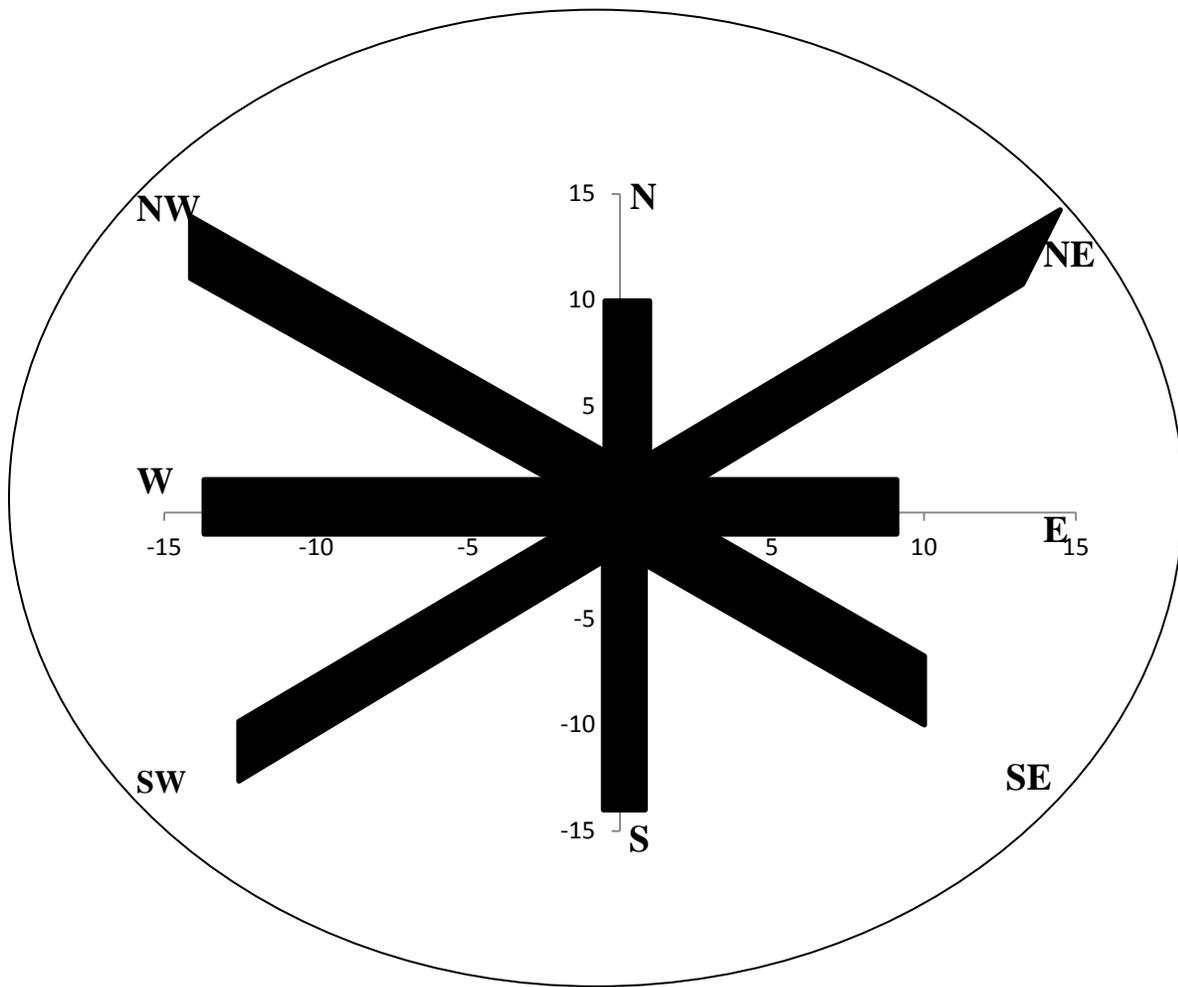


FIGURE 22: Illustration of the average rear orientation (%) of *P. oculifer* during the wet season

The overall rear orientation for *P. oculifer* during the wet seasons was predominantly in the westerly and southerly directions.

5. DISCUSSION

5.1 Home Range

5.1.1 Annual Home Ranges

The aim of the study was to determine the home range size, thermal profiles and orienting behaviour of the sympatric *S. pardalis* and *P. oculifer*. This aim was achieved by collecting data on geographic locations, thermal data from the weather station, temperature loggers and physical observations. It was hypothesized that the home range sizes of *S. pardalis* and *P. oculifer* differ significantly between species, sexes and between the wet and dry seasons. Within species, males were expected to have smaller home range sizes compared to the females as they roam over long distances in search for females for mating purposes.

Although the study found that on average, the overall home range size of *S. pardalis* and *P. oculifer* did not significantly differ, the home range sizes among individuals of both species differed and the annual home range size *P. oculifer* was twice that of *S. pardalis*. The home ranges of the two species were expected to not be significantly different as were the findings of the study; this is as a result of the site being a favourable environment for both species. The study site is part of the Kalahari desert and Branch (1998) stated that *P. oculifer* prefer the Kalahari sand (thus the genus name *Psammobates* = sand-loving); the species digs shallow refuges in sand and aestivate in these refuges during dry winter (Milstein, 1968). Importantly, it makes use of animal burrows as 'ready-made' retreats (Branch, 1988).

The study found that over the study period of 16 months, *P. oculifer* had an average annual home range of 64 ha irrespective of sex and size. Keswick (2012) observed that the home range sizes of males were 48 and 32 ha, and 26 and 27 ha for female *P. oculifer* in the western and eastern parts of the Benfontein Farm respectively. There was also great variation in Keswick's findings, the largest home ranges from his study was for two male *P. oculifer* tortoises that had annual home range sizes of 219.3 ha and 306.0 respectively. This is similar to the findings of from this study (299.0 ha for a male *P. oculifer*).

The larger home range size of both species observed was as a result of the variation between individual tortoises; Tortoises Psoc #5 male for instance had an annual home range size of 299.0 ha as a result of the long distance movements undertaken by this exceptional individual tortoise. Both sexes have the capacity to wander over large areas, despite their small size (Keswick, 2012). This study observed that the males wandered more than their female counterparts.

Several other studies (Rose & Judd, 1975; Geffen & Mendelssohn, 1988; Diemer, 1992; O'Connor *et al.*, 1994; Nieuwolt, 1996; McMaster & Downs, 2009) also observed that large inter-individual variation is a common trend in testudinid home range studies.

Additionally, tortoise home range size tend to be larger mostly in areas where resources are limited, patchy and where there is evident competition in cases of sympatric species (Geffen & Mendelssohn, 1988). McMaster & Downs (2009) support the findings of the current study as they stated that home ranges of testudinid populations in arid or harsh environments tend to be large.

Stigmochelys pardalis was found to have an average annual home range of 20 ha. The largest individual annual home range recorded for *S. pardalis* was 58 ha, for a medium sized male and the smallest individual home range recorded was 1.0 ha for a juvenile. A study by McMaster & Downs (2009), found that a medium sized male *S. pardalis* with a mean weight of 10kg and a Straight Carapace Length (SCL) of 400mm had a mean annual home range of approximately 200 ha.

All individual annual home range sizes for *S. pardalis* observed from this study were less than 60 ha. This can be attributed to the size and imbalance in the sample population; from the total sample population of 8 *S. pardalis* individuals, 6 were female, 2 were juveniles and only 1 was a medium sized male weighing 3kg on average. Branch (1988) indicated that in testudinid species, males tend to have larger home ranges than their female counterparts as they often roam over larger areas in search for mates. However, the annual sampling regime in McMaster & Downs (2009) was based on two locations per day; while in this study it was once per week and this might also have affected the home range estimates of *S. pardalis*.

Based on the findings, the similarity between the home range sizes of *P. oculifer* and *S. pardalis* indicates that within the boundary of tortoises' annual activity areas (defined by MCPs), both tortoises species had a high degree of space's utilisation (Keswick, 2012; McMaster & Downs, 2009).

5.1.2 Seasonal Home Ranges

Findings from this study have shown that the home range sizes were larger during the wet season compared to the dry season for both species. McMaster & Downs (2009) found that home ranges were smaller during the dry season because the lower temperatures affect home range greatly as a consequence of the lower activity of tortoises during this season (McMaster, 2001). Inactivity of tortoises and other ectothermic organisms due to lower temperatures is also associated with limited food resources during the dry seasons as well as the difficulty in finding mating partners.

Home range sizes were larger during the wet seasons because temperatures were conducive enough to allow tortoises to carry out different activities. McRae, *et al* (1981) stated that home ranges in seasons associated with higher temperatures are higher as they can be attributed to seasonal migration, escape from human disturbance, or searching for forage, mates, cover sites, or nest sites. The home range findings from this are similar to those of McRae *et al.* (1981). The study found that *G. polyphemus* in south western Georgia had home ranges that significantly varied seasonally and this variation was largely due to social interaction. McRae *et al.* (1981) found that the Gopher tortoises were active during the spring and summer seasons. Level of activity reduced as autumn approached and eventually stopped during winter.

Keswick (2012) observed a significant difference between the seasonal 100% MCPs. Spring MCPs were the largest (105.4 ha) and winter MCPs were the smallest (1.39 ha).

5.1.3 Home Range Overlap

Home range overlap was evident between species and sexes. Diemer (1992) studied the home range of *G. polyphemus* and found that there was a difference between sexes, with female home ranges not overlapping but male home ranges overlapping with other home ranges of both sexes.

This is contrary to the findings of this study as it was found that home ranges of female tortoises from both species overlapped. On several occasions, individuals from both species were found under the same vegetation cover. Home range overlaps between males and female of both species was very common, and similar to several other studies on different tortoise species (Rose & Judd, 1975; Chelazzi & Calzolari, 1986; Els, 1989; Hailey, 1989). These studies concluded that many tortoise species have home ranges that overlap with one another but it is not an indication of territoriality or home range defense.

McMaster & Downs (2009) found that there was great individual variation in the amount of home range overlap of *S. pardalis* as individuals of different size and sex did have overlapping home ranges to varying degrees across all seasons. Similarly, high degree of overlap was observed between home ranges of *Testudo kleinmanni* and it was concluded that this showed lack of defense of territories and resources (Geffen & Mendelsohn, 1988). Keswick (2012) also observed a similar trend in home range overlapping of *P. oculifer*. Frequencies of individual *P. oculifer* with 100% MCP overlap differed among seasons with more home ranges overlapping in spring than in winter. These findings all support the findings from the current study.

5.2 Temperature

For the temperature aspect of the study, it was hypothesized that the iButton and ambient temperatures would differ significantly. It was also expected that the temperature would be significantly different between the dry and wet seasons. Additionally, based on the thermal inertia concept, *S. pardalis* was expected to maintain its preferred body temperature compared to *P. oculifer*.

Findings from the study indicate that there is no significant difference between the temperature recorded by the iButtons and the weather station. A two-way ANOVA statistical test have also shown that temperatures recorded from the shell, iButton, surface and meteorological did not differ significantly.

Most testudinid thermal studies (McMaster & Downs, 2009, 2013; Gerlach, 2005; Boycott & Bourquin, 2000; and Diemer, 1992) had surgically implanted thermal loggers in the cloaca of the animals. Most studies also only focused on the daily thermal activities of the tortoises (McGinnis & Voigt, 1971; Meek, 1984; Loehr, 2002) and very few looked at the seasonal patterns. This is different from this study where thermal loggers (iButtons) were placed on the carapace of the tortoises. In comparison to the cloacal implanted thermal loggers, the iButtons were highly affected by external factors and cannot be considered as a representative of the shell temperature.

It was found that for both species, the temperature variables did not differ however, graphic representations suggest that the variables are not the same and they are all dependent on the ambient temperature (recorded by the weather station). In their study, McMaster & Downs (2013) found that *S. pardalis* followed the classic daily pattern of chelonian thermoregulatory behaviour (Cloudsley-Thompson, 1970; McGinnis and Voigt, 1971; Lambert, 1981; Meek, 1984; Loehr, 2002), where they exhibit more bimodal activity patterns in summer and unimodal activity patterns in winter.

McMaster & Downs (2013) further stated that *S. pardalis* had body temperatures lower than the ambient temperatures over the course of the day in summer while in winter *S. pardalis* were active at lower body temperatures, and at lower ambient temperature than in summer. Studies by Branch (1984), Pulford *et al.* (1984), Meek (1988), Geffen & Mendelsohn (1989), Hailey & Coulson (1996b), Loehr (2002) and Ramsay *et al.* (2002) have all suggested that activity in tortoises are initiated when the tortoise has reached an optimal body temperature and that tortoises will remain inactive until the body temperature has been reached. Perrin & Campbell (1981) and Hailey &

Loveridge (1998) concluded that 28°C is the optimal body temperature for *S. pardalis*. A conclusion cannot be drawn on the optimal body temperature of *P. oculifer* from the findings of this study as more studies still need to be conducted in order to verify this.

Contrary to this, McMaster & Downs (2013) found that *S. pardalis* initiated activities at different temperature range depending on the ambient temperature during a particular season. Meek (1988) also concluded similarly when he argued that seasonal changes in recorded body temperatures of *T. hermanni* do not indicate seasonal differences in optimal means or ranges, but they probably reflect the body temperature tolerated for a specific activity.

In his study on *P. oculifer*, Keswick (2012) reported that when the tortoises were found walking and feeding (active), the recorded temperatures were closely related to those recorded as the ambient and ground/surface temperatures. As such, there was no observed significant difference between the temperatures recorded for different behaviours.

5.3 Orientation

The direction in which an organism will orient itself is greatly determined by the temperatures at a given time. For the rear orientation aspect of this study, it was hypothesized that tortoise exposure to the sun between different seasons and weather conditions differed.

Although studies on refuge orientation in testudinids are scarce, a study by McMaster & Downs (2006) on the South African *S. pardalis* found that the species tend to be orientated S or SW during the dry season. In his study, Keswick (2009) looked at the orientation directions between sexes seasonally and found that the species' mean direction was dominantly E for both males and females.

Cunningham & Simang (2006) found that *P. oculifer* dominantly oriented its rear side towards the easterly directions (E/NE/SE) (38.2%) followed by a southerly orientation (S/SE/SW) (30.9%). They further discussed that orientation of the carapace towards the E assists basking by raising the temperature to the optimum required for foraging.

Cunningham & Simang (2008) conducted a similar study on *Psammobates tentorius veroxii* in the southern part of Namibia and found that the species' orientation while in a resting place varied between morning and afternoon during the wet season. Results from the study indicate that orientation was mostly N (including NE and NW) and E. It was further observed that orientation during the dry season was mostly towards the E (including NE and SE) and N; and did not change during the dry season due to the inactivity of the individuals during this period.

In other studies, the small arid zone tortoise, *Testudo kleinmanni*, was observed to be oriented mostly in the E and S directions of their rested places bushes during winter and spring in the Negev desert and Benfontein (Geffen & Mendelssohn, 1989).

The easterly orientation directions recorded during the dry seasons from this study show that the orientation could have been done as a thermoregulatory strategy. Geffen & Mendelssohn (1989) stated that testudinids tend to often orient their bodies in the directions of the sunrise or sunset. Cunningham & Simang (2008) supported this by stating that testudinids may position themselves when going into a resting to enable them to reach an optimum temperature quickly. Orientation

towards the sun in the morning hours (N and E) can suggest that tortoises orient themselves in that to ensure that they receive the heat of the morning sun to commence foraging while still relatively cool in the morning. Orientation away from the sun (E and S) during the heat of the day is probably to avoid overheating during this period.

6. CONCLUSION AND RECOMMENDATIONS

6.1 Conclusion

Home ranges of both *P. oculifer* and *S. pardalis* did not significantly differ between species. Males however, tend to have larger home ranges compared to females. The fact that there was evident interspecific and intraspecific home range overlap, implies that both species are not territorial. Seasonally, home ranges for both species were larger during the wet season and smaller during the dry season. This is in line with most findings on research done on *P. oculifer* and *S. pardalis*. The null hypothesis which stated that there is no significant difference between ambient, shell, iButton and surface temperatures associated with the tortoises, is thus accepted.

Thermal conditions experienced by the tortoises did not significantly differ between seasons. However, high temperatures were observed during the wet seasons and low temperatures during the dry season. Temperatures recorded from the iButton, shell, surface and ambient all showed a positive relationship. In this regard, the null hypothesis is accepted.

Findings from the study indicate that the north-easterly direction was the mean rear orientation direction throughout the study period. Seasonally, rear orientation directions differed and were not uniform; during the dry season, northerly directions were the most dominant for *S. pardalis* rear orientation while northerly and easterly were most dominant for *P. oculifer* rear orientation. These results indicate that there was no uniform direction for orientation amongst the species and even seasonally and thus the null hypothesis is accepted.

6.2 Recommendations for future work

To strengthen the current understanding, knowledge on extent of home range overlap is essential. Long-term studies on home range and temperature (with continuous monitoring) are essential in obtaining an accurate home range size and preferred body temperatures. A study on preferred diet of both species should also be conducted to determine the differences between the species' diets.

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8. APPENDICES

Data Sheet: Hohewarte Farm Tortoise Study, Windhoek

Date: _____ Capture: _____
 Observer: _____ Tortoise Nr: _____
 Time: _____ Species: Leo • Tent • Others
 Sex: M • F Permanent shell marking: _____
 Weight:.....g

GPS Position: S: _____ E: _____ Alt:.....m

Waypoint: _____

Environmental Conditions

Parameters					
Sky Conditions <i>(please circle)</i>	Temperature	Soil <i>(please circle)</i>	Solar Radiation	Body Measurements	
Sunny	T _{g.surface} =.....°C	Wetw.m ²	Weight=.....g	Claws: Front= Back=
Partly cloudy	T _{g.laid up} =.....°C	Dry		SCL=.....mm	
Heavy cloudy	T _{tortoise shell} =.....°C			SW=.....mm	Margins: Left= Right=
Rainy	T _{tortoise skin} =.....°C			SH=.....mm	
Drizzle	T _{air} =.....°C			PL=.....mm	Shell damage:
Windy				AG=.....mm	<i>Please indicate on the diagrams below</i>

Annual Rings (years): 6-7 • 8-9 • 10-11 • 12-13 • 14-15 • 16-17 • 18-19 • 20-21 • 22-23 • 24-25 • 26-27
 • 28-29 • 30-31 • 32-33 • 34-35 • 36-37 • 38-39 • Other

Behaviour

Open *(circle)*: • Walking • Feeding • Resting • Others

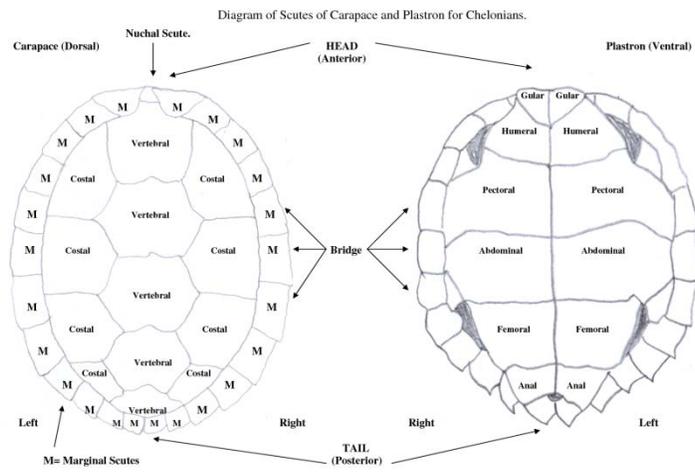
Laid up (undercover):

 Shade *(circle)*: Partial • Full

 Shade Species:.....(Note: If unknown, please take a sample)

✚ Plant height:..... cm

✚ Others:



Comment (include any other observations):.....
.....

Micro-climate Data Analysis
Location: Hohewarde
Date Range*: December 2013 – April 2015

By: Michealene Iaukea-Lum

For: Professor Emeritus James O. Juvik and Dr. Jill Heaton

This document is a simple write up and analysis of currently worked data files. Not all files have been completed at this time.

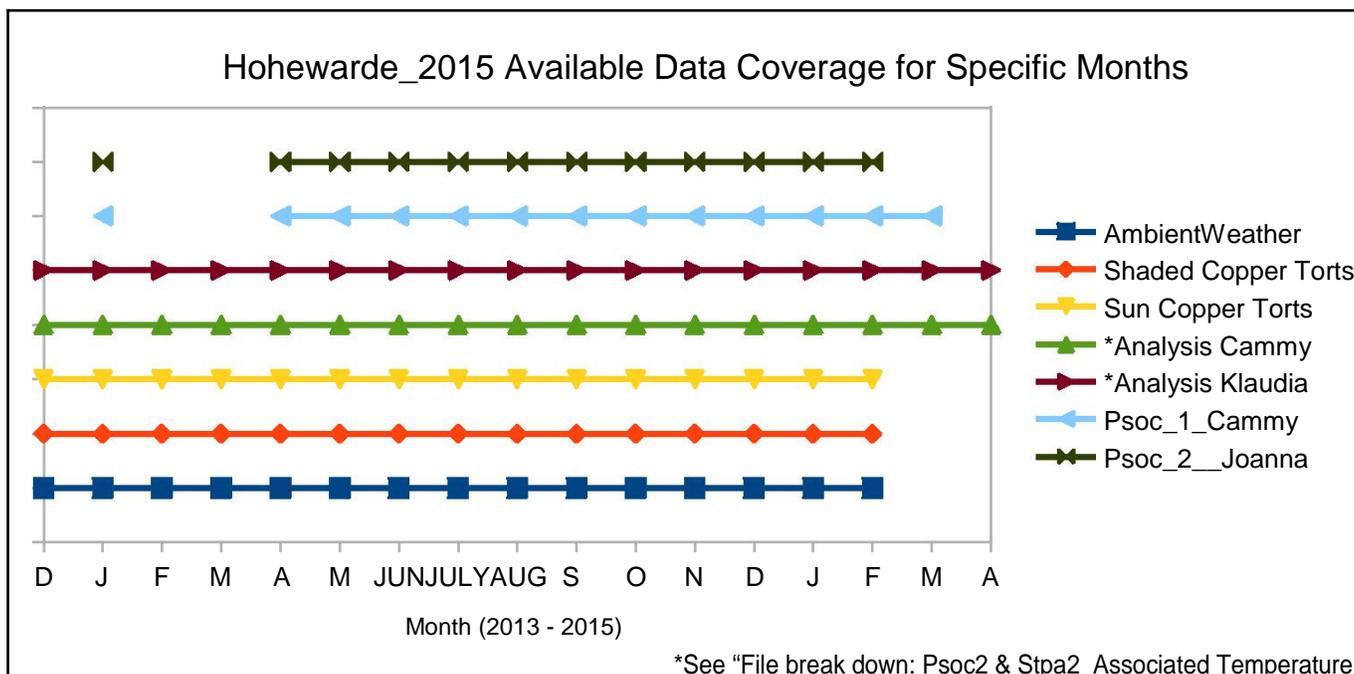
*Date Range is not available for all files. For specific ranges see data coverage graphs

General Information

Completed and Pending Files

Analysis complete for the following files:	Analysis pending for the following files:
Hohewarde_AmbientWeather_20150323 Hohewarde_ShadedCopperTorts_20150323 Hohewarde_SunCopperTorts_20150323 Psoc2 & Stpa2_Associated Temperature Broken down: Analysis Cammy and Analysis Klaudia Psoc_1_Cammy_Hohewarde_20150315 Psoc_2_Joanna_Hohewarde_20150227	Psoc_3_Heike_Hohewarde_20150313 Psoc_5_Eillo_Hohewarde_20150215 Psoc_5_Eillo_Hohewarde_20150323 Psoc_6_Olla_Hohewarde_20150323 Psoc_7_Valentine_Hohewarde_20150313 Psoc_8_Jill_Hohewarde_20150323 Stpa_2_Klaudia_Hohewarde_20150313 Stpa_3_ThreeLegs_Hohewarde_20150315 Stpa_4_Willian_Hohewarde_20150315 Stpa_5_Gomez_Hohewarde_20150323 Stpa_10_Alicia_Hohewarde_20150323 Stpa_11_NoFire_Hohewarde_20150323 Stpa_14_NewPandu_Hohewarde_20150323 Stpa_15_Newlvy_Hohewarde_20150323 Stpa_17_Sugar_Hohewarde_20140323 Stpa_18_Kiester_Hohewarde_20150129 Stpa_19_Kalinda_Hohewarde_20150323

Data coverage

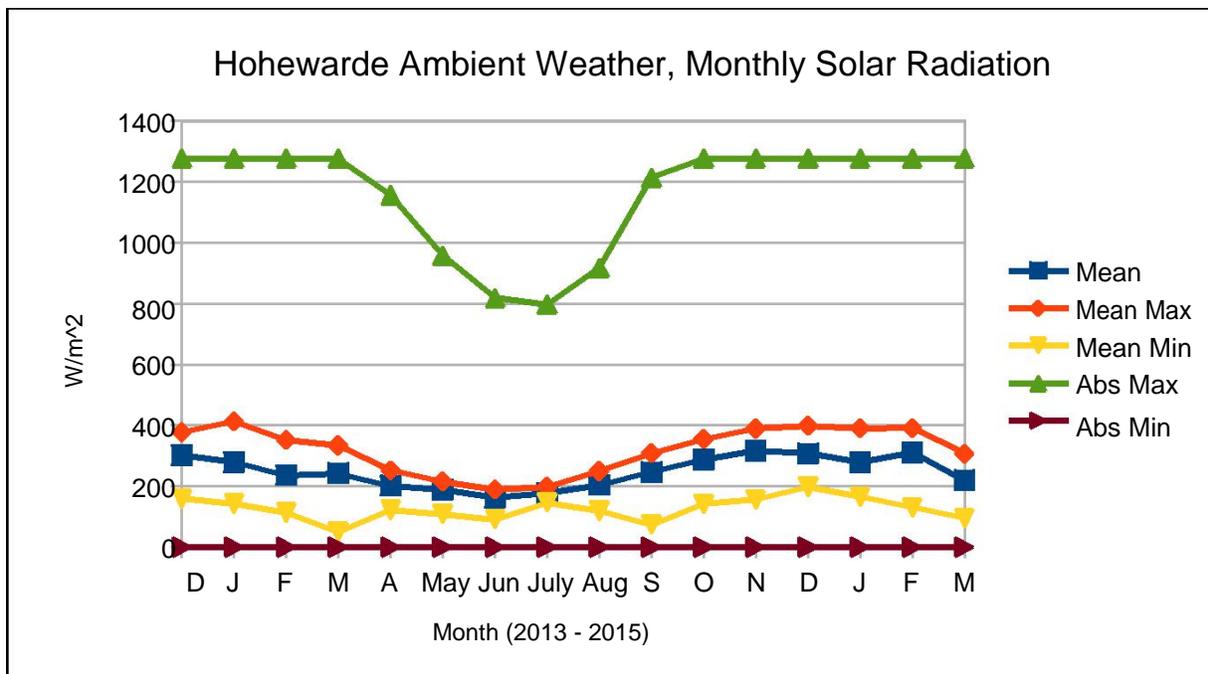


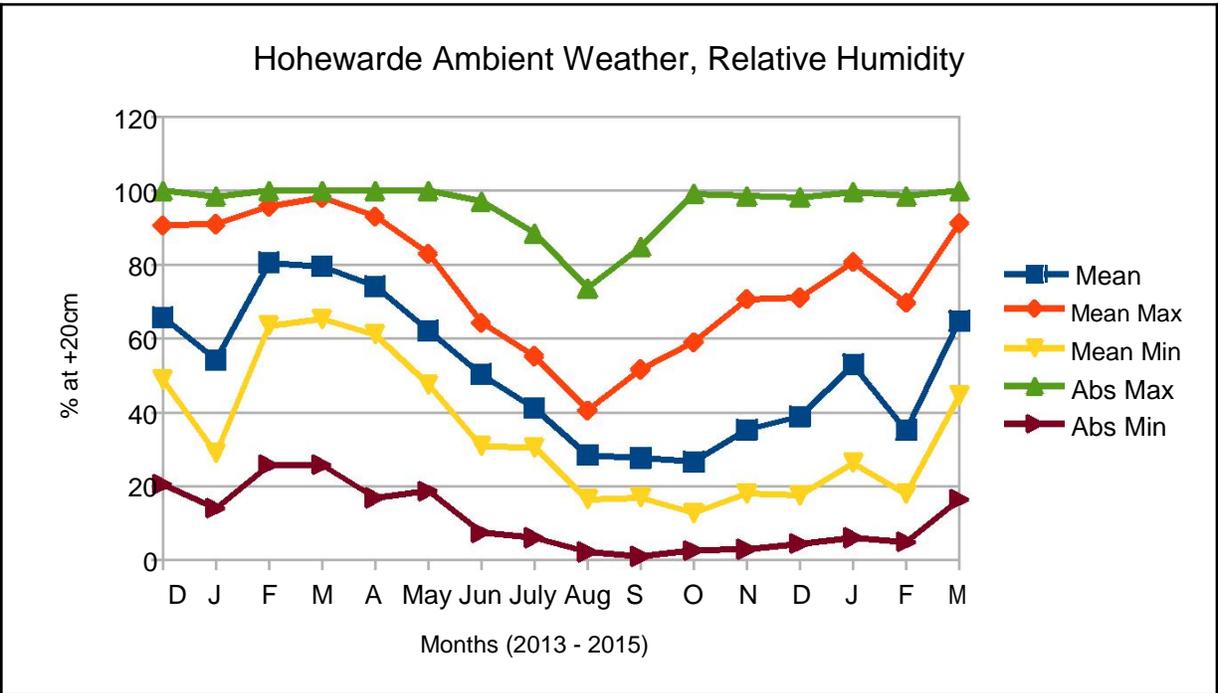
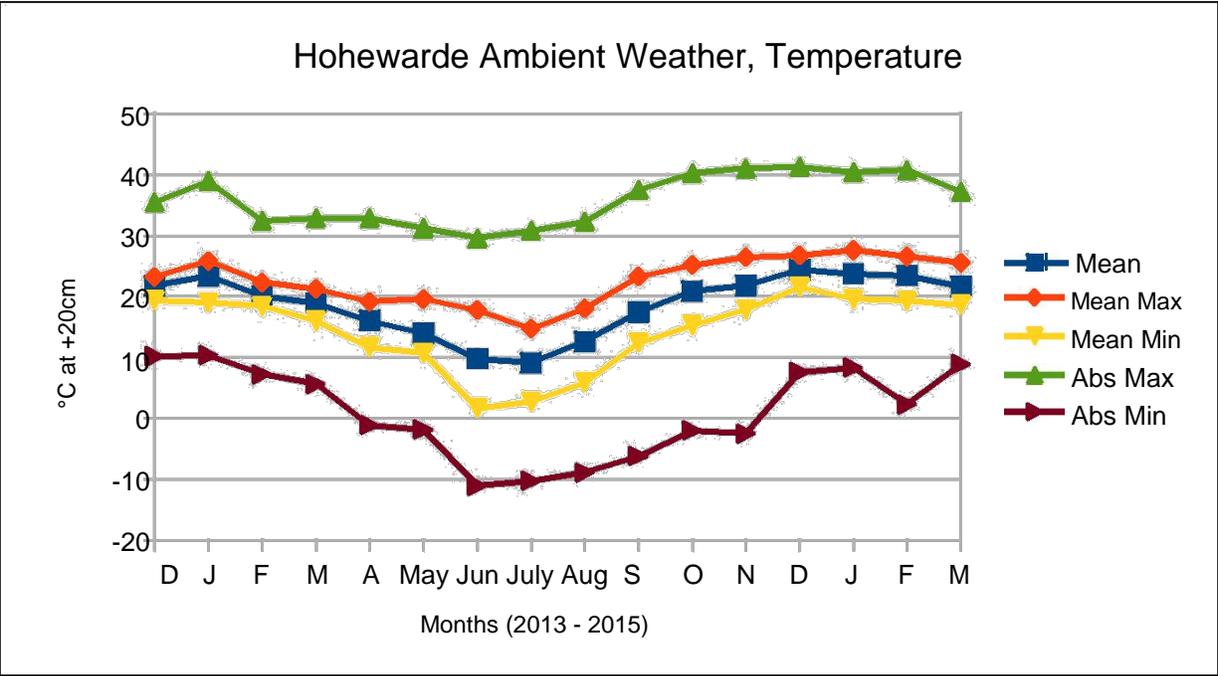
File break down

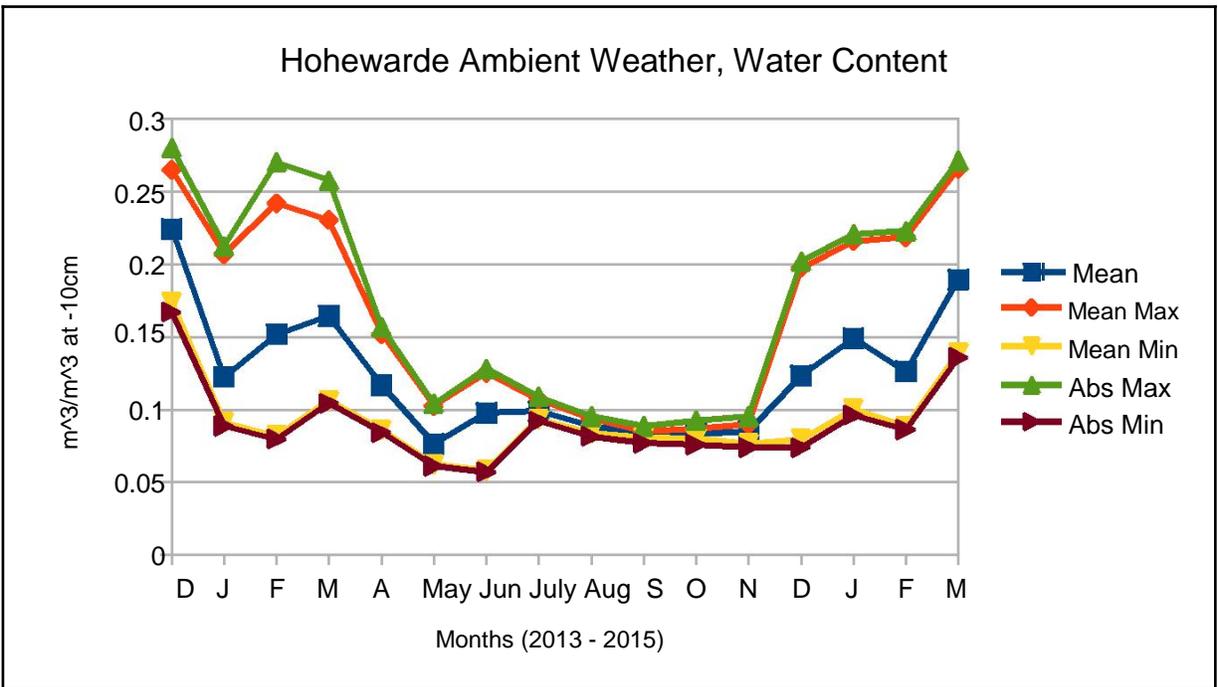
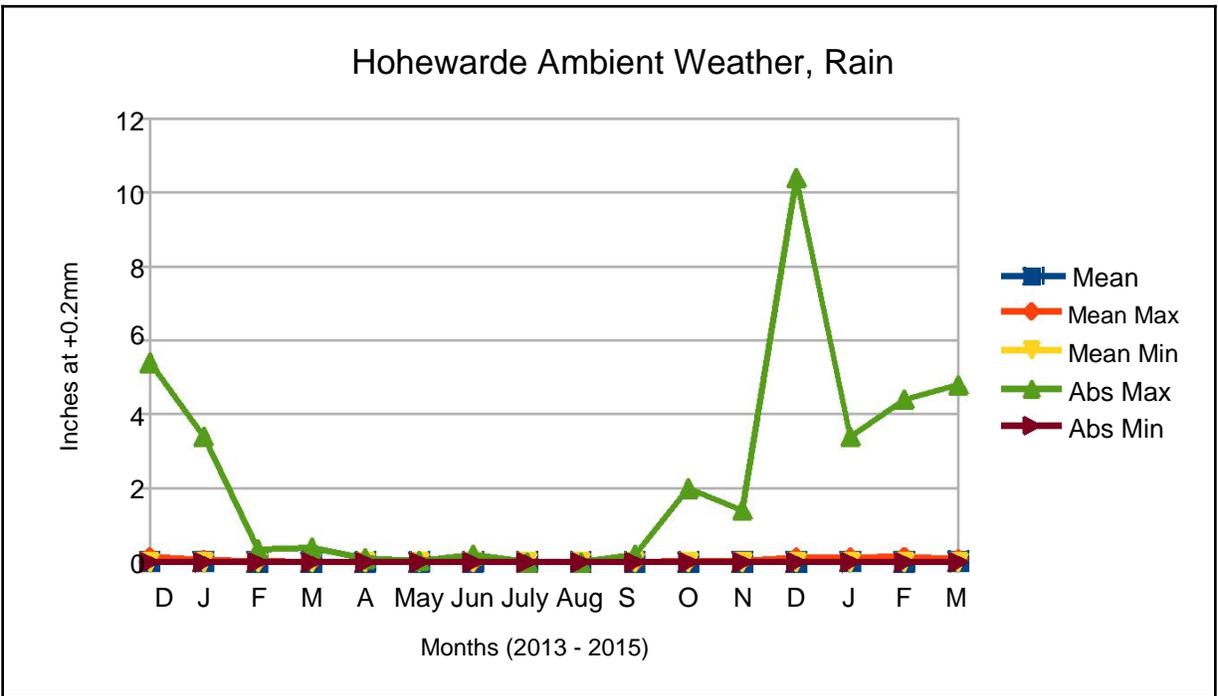
Hohewarde_AmbientWeather_20150323

Attributes within the file: Solar Radiation, W/m²
Temp, °C (LBL: +20cm)
RH, % (LBL: +20cm)
Rain, in (LBL: 0.2mm)
Water Content, m³/m³ (LBL: -10cm)

Calculated for each attribute: Monthly and daily: mean, mean max, mean min, absolute max, and absolute min



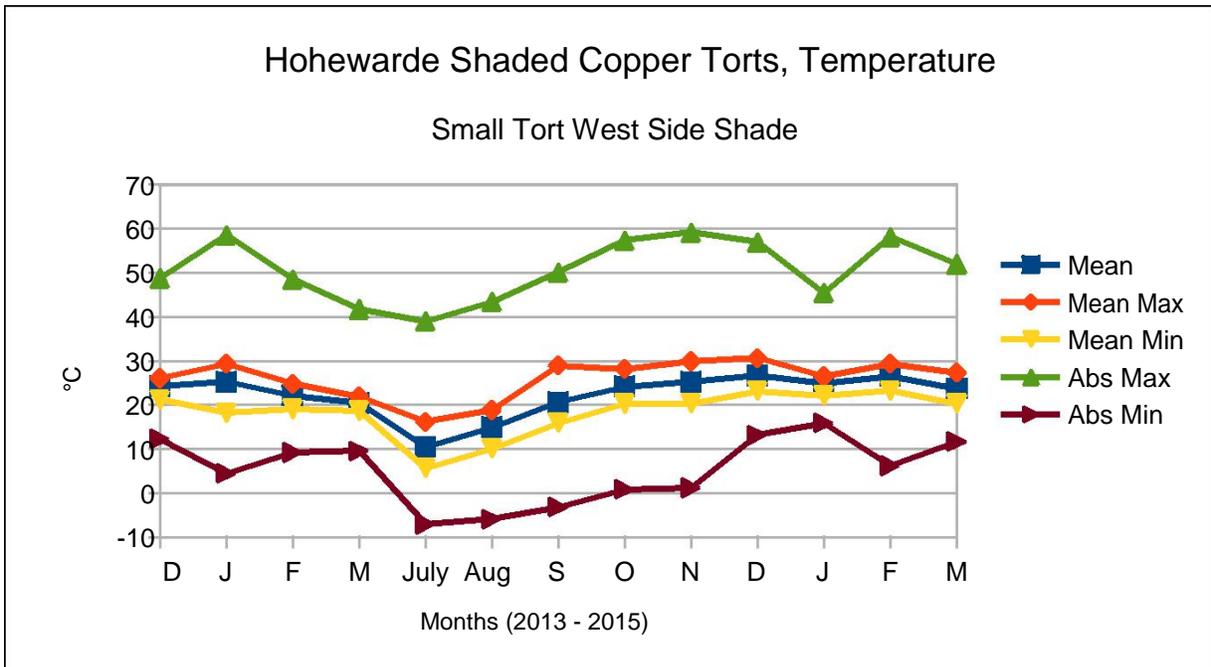
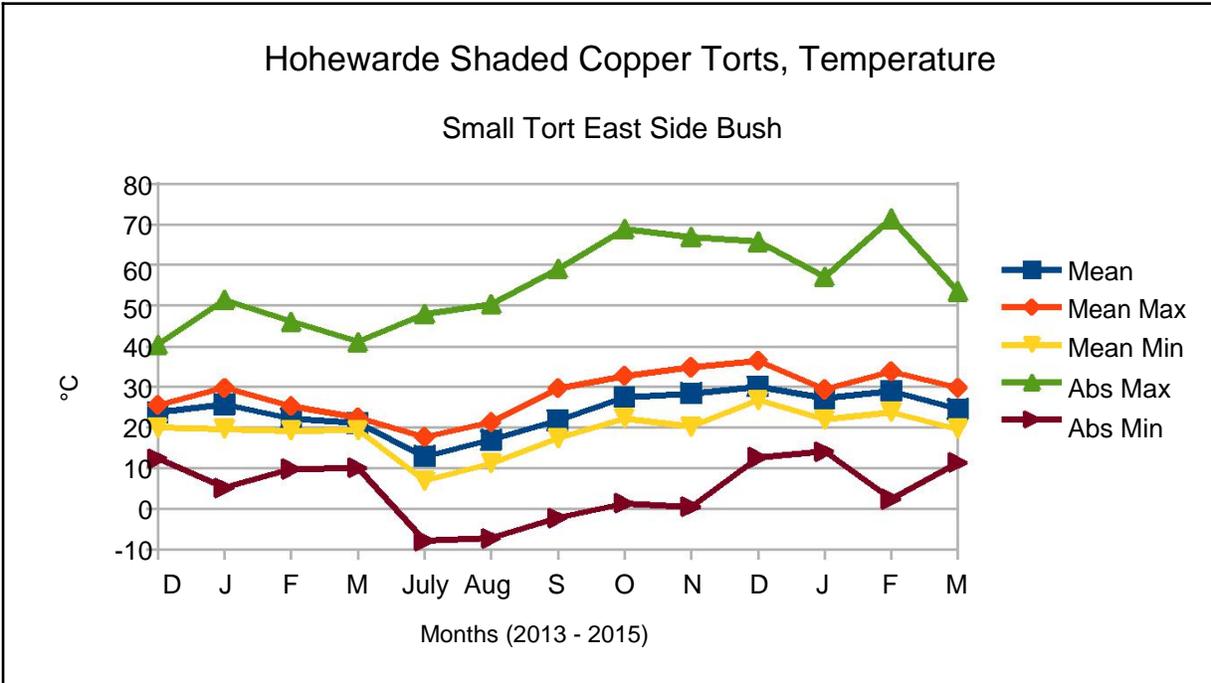




Hohewarde_ShadedCopperTorts_20150323

Attributes within the file: Temp, °C (Small Tort East Side Bush) Temp,
°C (Small Tort West Side Shade)

Calculated for each attribute: Monthly and daily: mean, mean max, mean min,
absolute max, and absolute min

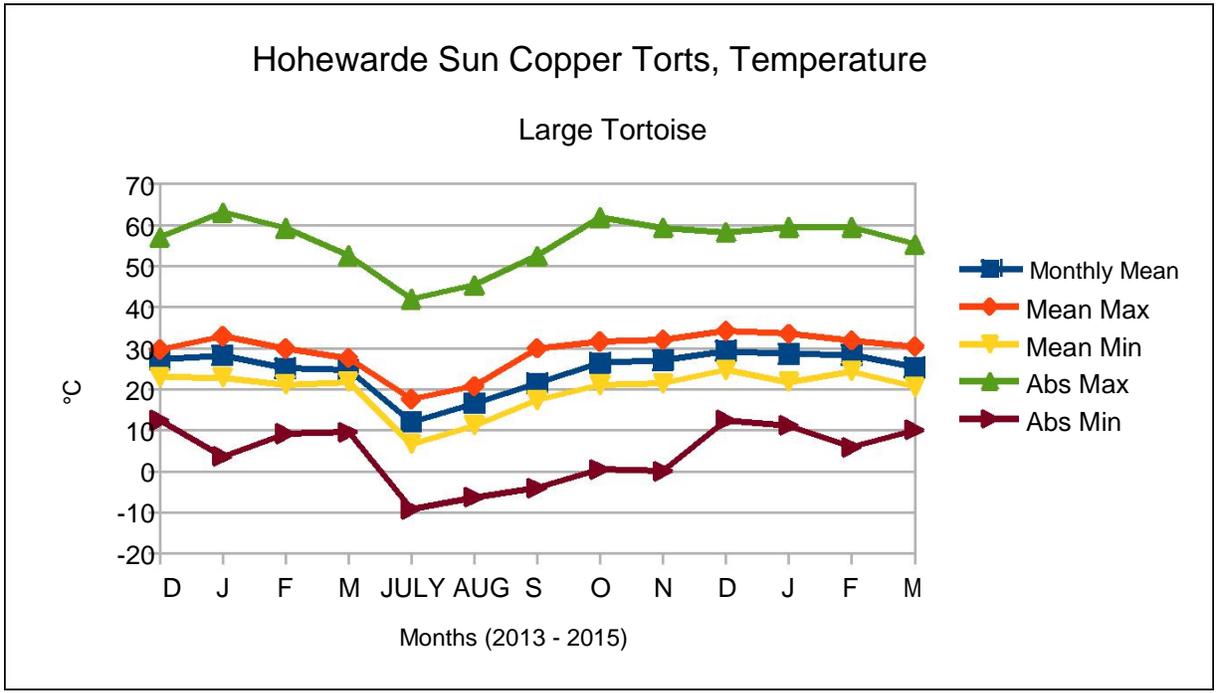
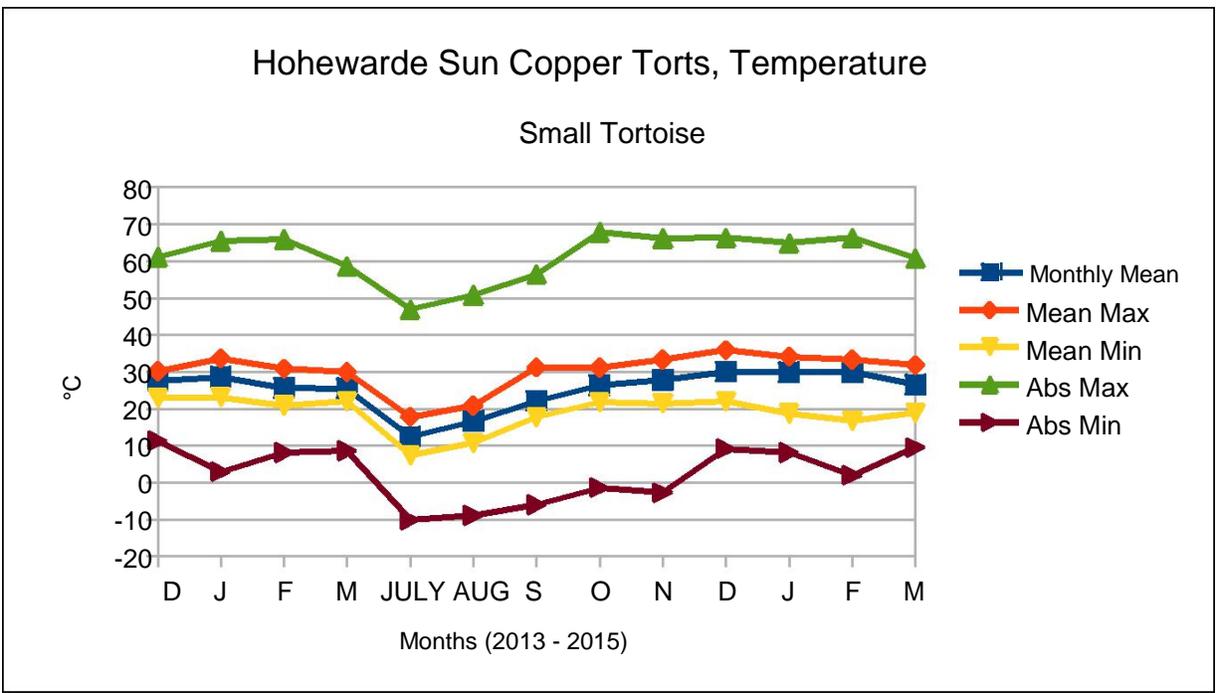


Hohewarde_SunCopperTorts_20150323

Attributes within the file: Temp, °C (Small Tortoise)

Temp, °C (Large Tortoise)

Calculated for each attribute: Monthly and daily: mean, mean max, mean min, absolute max, and absolute min



Psoc2 & Stpa2_Associated Temperature

Broken down to **Analysis Cammy** and **Analysis Klaudia** with the following calculations for each. (T = Temperature)

Tsurface vs TiButton
 vs Tshell
 vs Tlaidup
 vs Tair
 vs TcopperModelsShadeEast
 vs TcopperModelsShadeWest
 vs TcopperModelsSunSmall vs
 TcopperModelsSunLarge

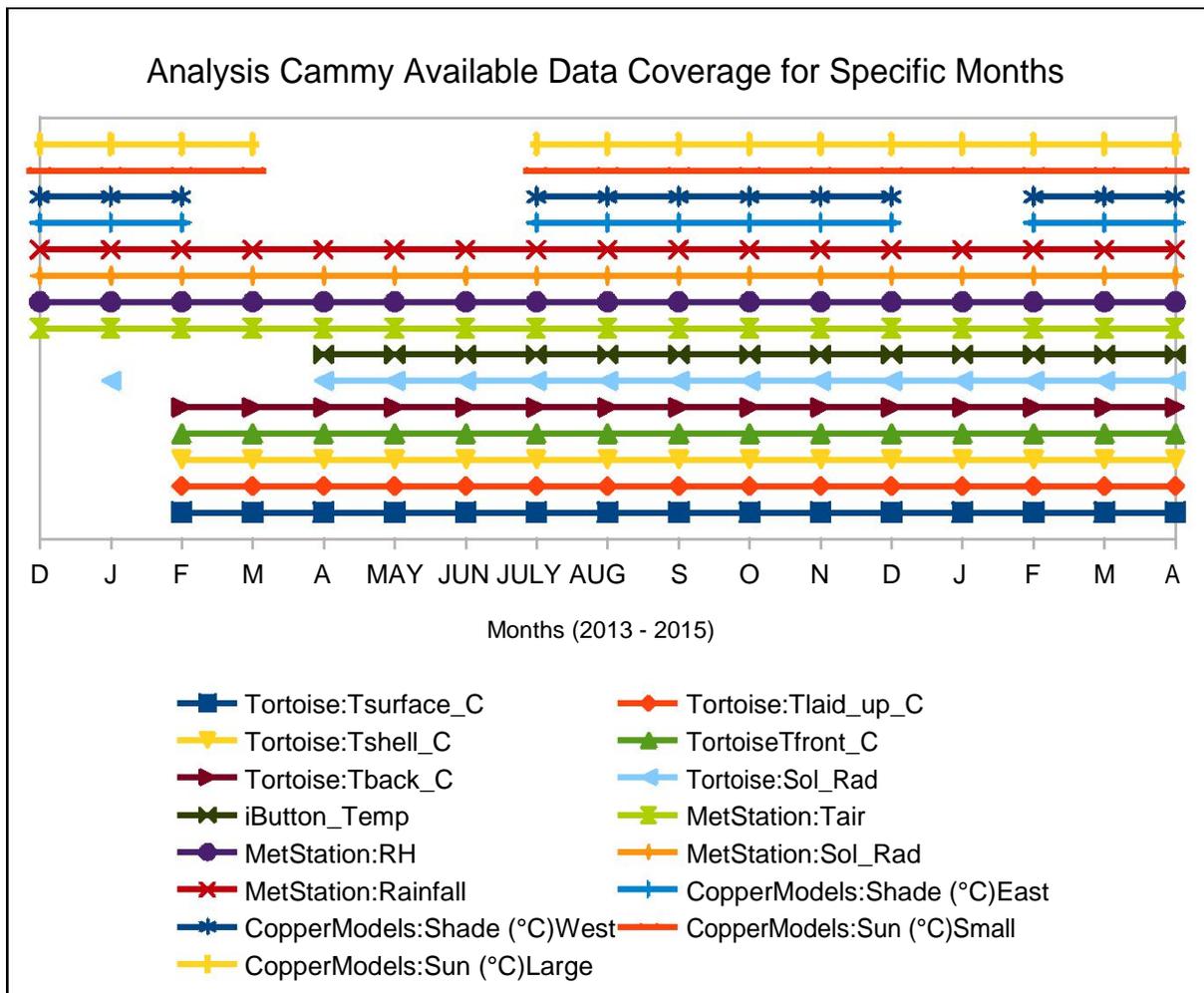
TiButton vs Tshell
 vs Tair

SolRad (Met Station) vs TiButton

Tsurface vs Tafb (Tafb: Temperature average of front and back)

TiButton vs Tafb (Tafb: Temperature average of front and back)

Analysis Cammy



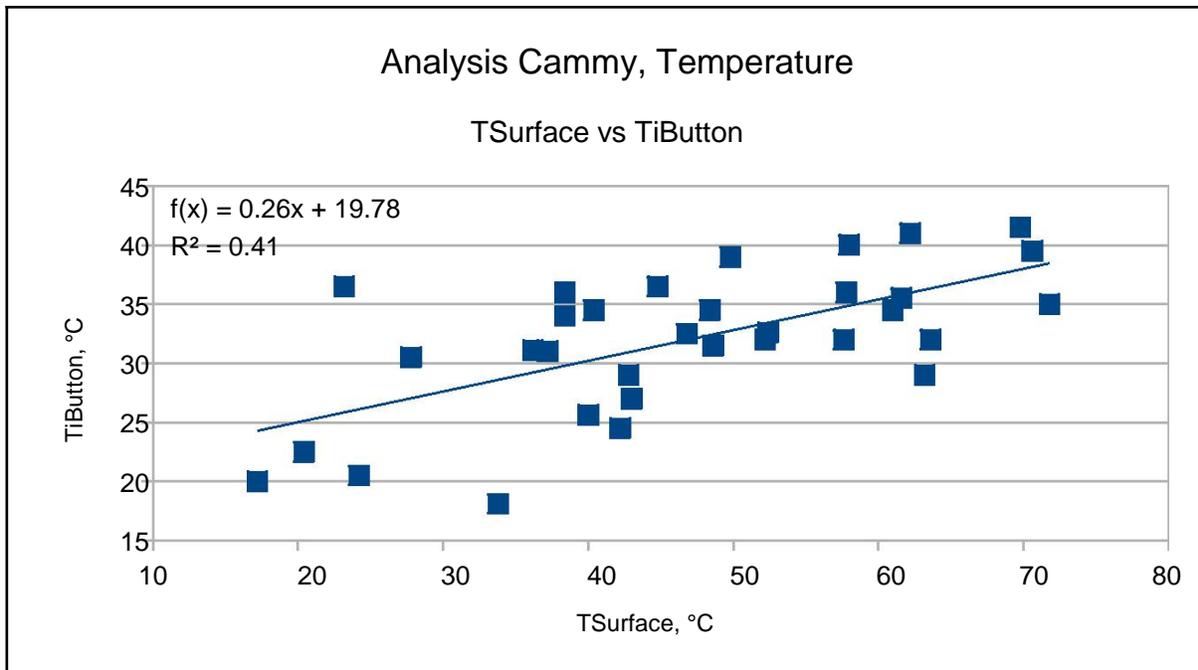
Graph File: Analysis Cammy

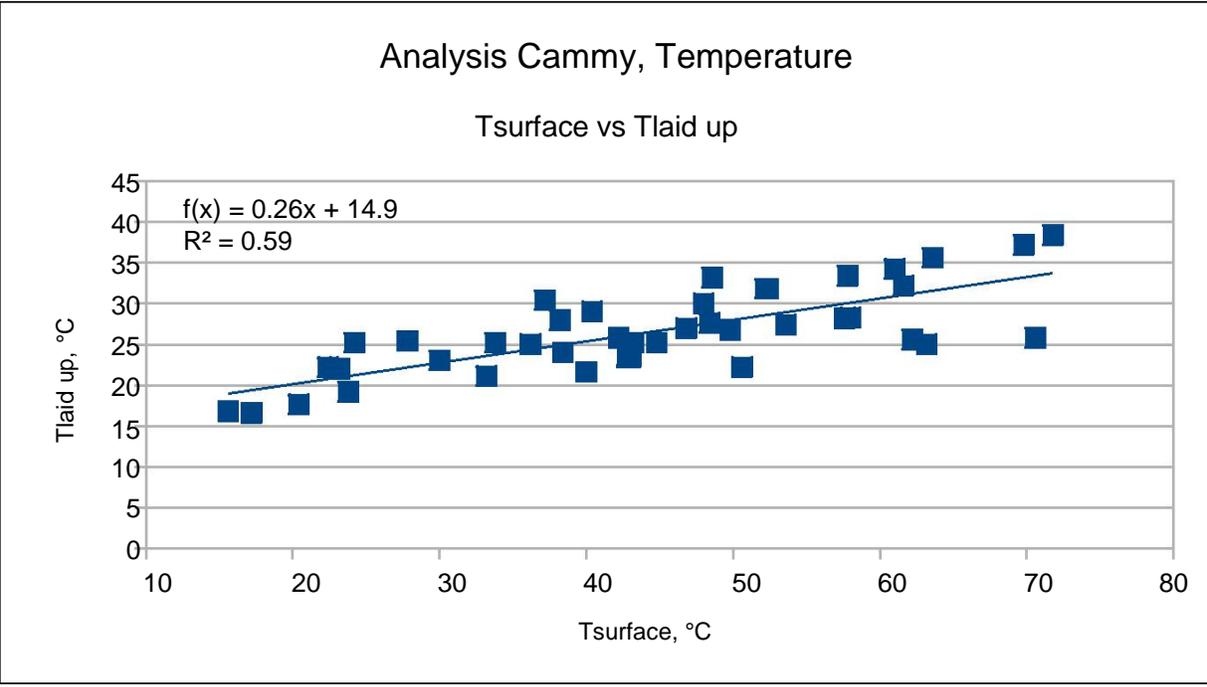
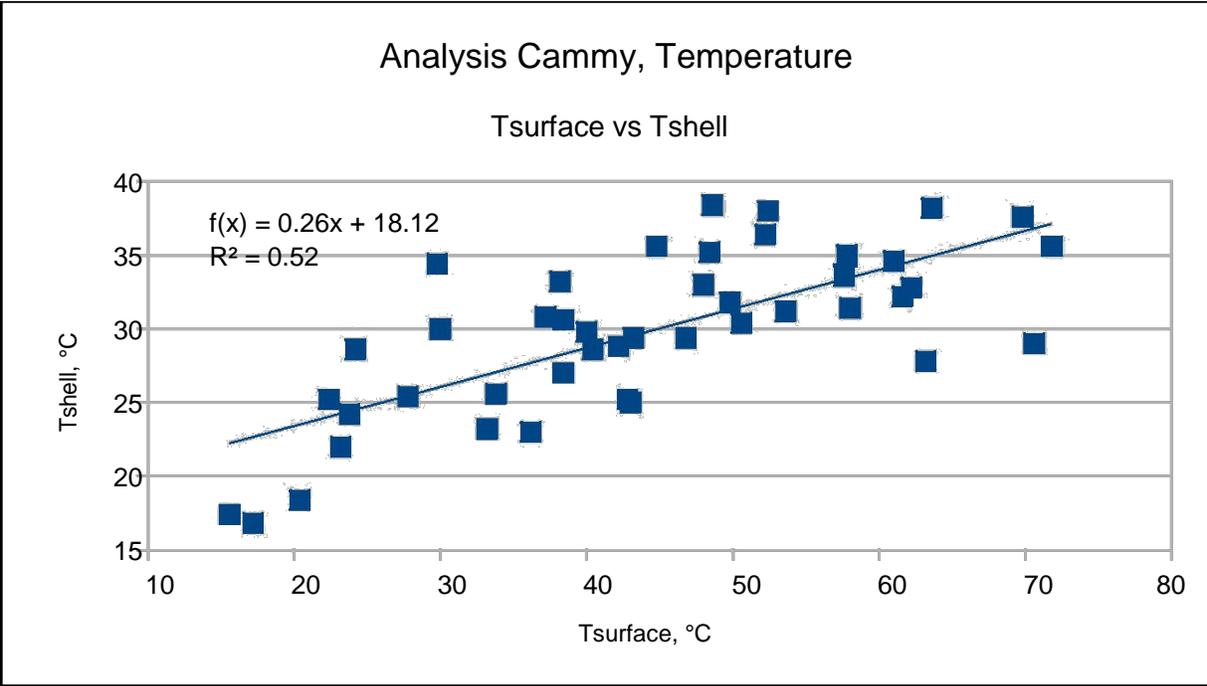
Data Points

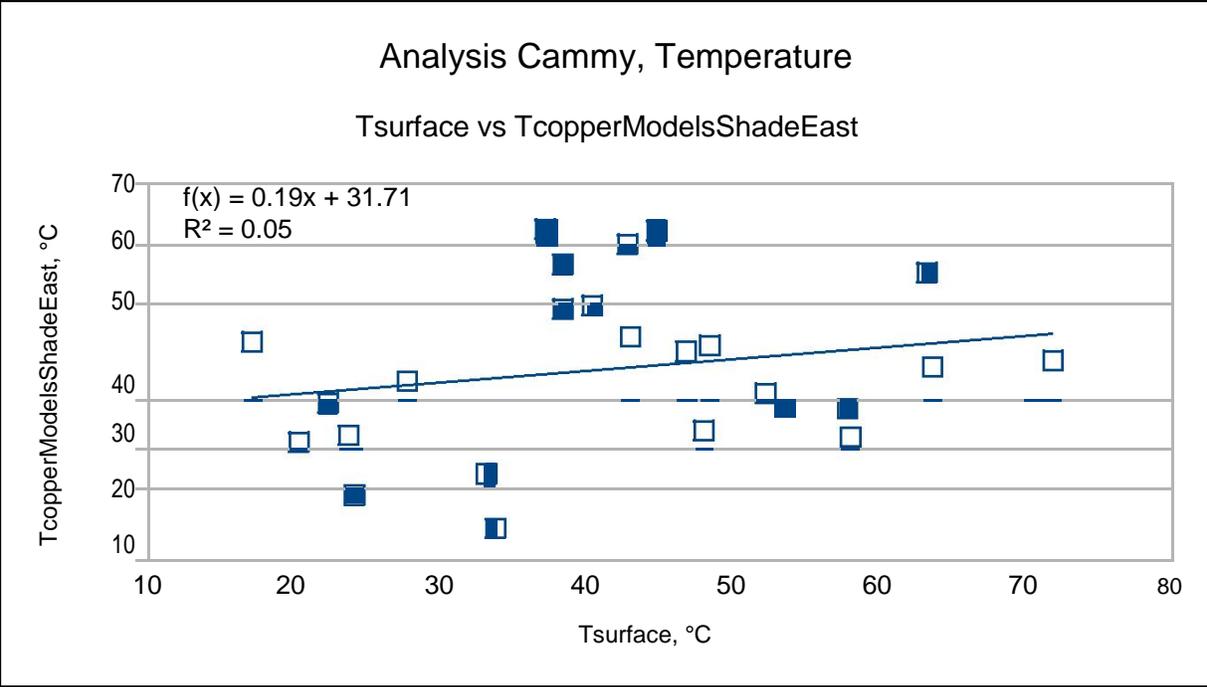
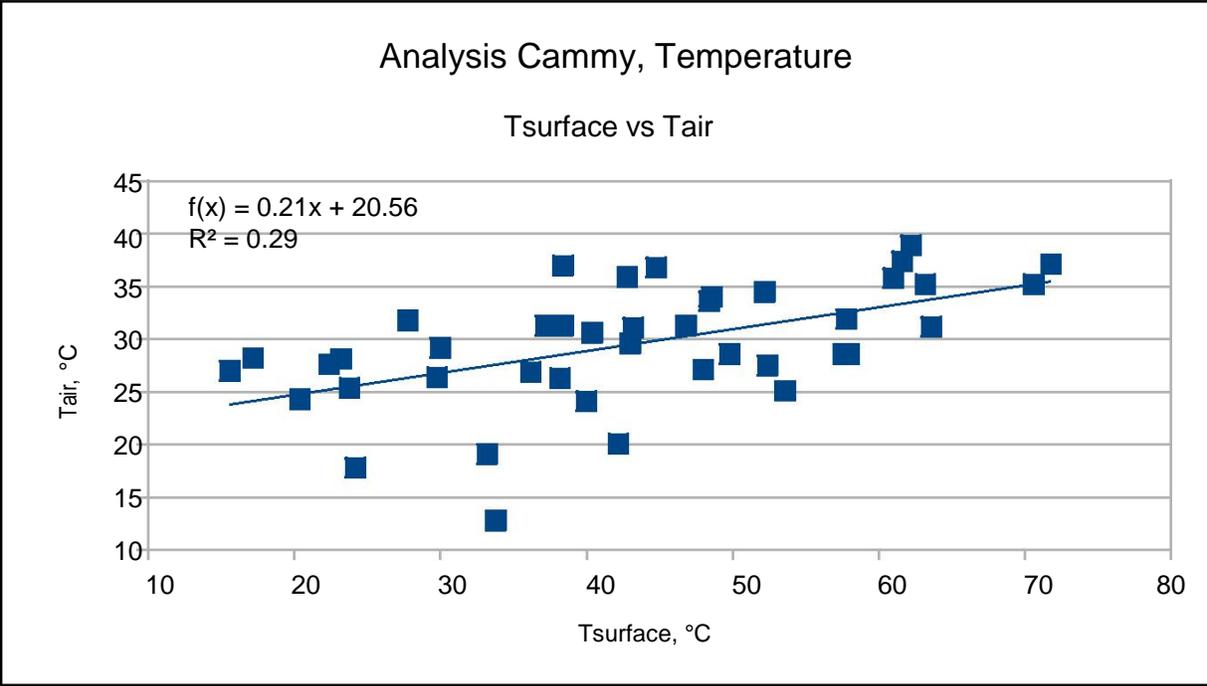
R² Value

Equation

	Data Points	R ² Value	Equation
1 Tsurface vs TiButton	33	0.412	$f(x) = 0.261x + 19.777$
2 Tsurface vs Tshell	44	0.523	$f(x) = 0.265x + 18.122$
3 Tsurface vs TlaidUp	43	0.586	$f(x) = 0.263x + 14.901$
4 Tsurface vs Tair	42	0.294	$f(x) = 0.208x + 20.563$
5 Tsurface vs TcopperModelsShadeEast	26	0.052	$f(x) = 0.191x + 31.714$
6 Tsurface vs TcopperModelsShadeWest	26	0.402	$f(x) = 0.379x + 20.061$
7 Tsurface vs TcopperModelsSunSmall	31	0.151	$f(x) = 0.314x + 30.764$
8 Tsurface vs TcopperModelsSunLarge	31	0.184	$f(x) = 0.277x + 28.482$
9 TiButton vs Tshell	33	0.283	$f(x) = 0.493x + 0.283$
10 TiButton vs Tair	32	0.488	$f(x) = 0.708x + 8.08$
11 SolRad vs TiButton	33	0.265	$f(x) = 0.008x + 26.006$
12 Tsurface vs Tafb	41	0.542	$f(x) = 0.240x + 17.240$
13 TiButton vs Tafb	31	0.366	$f(x) = 0.465x + 13.436$

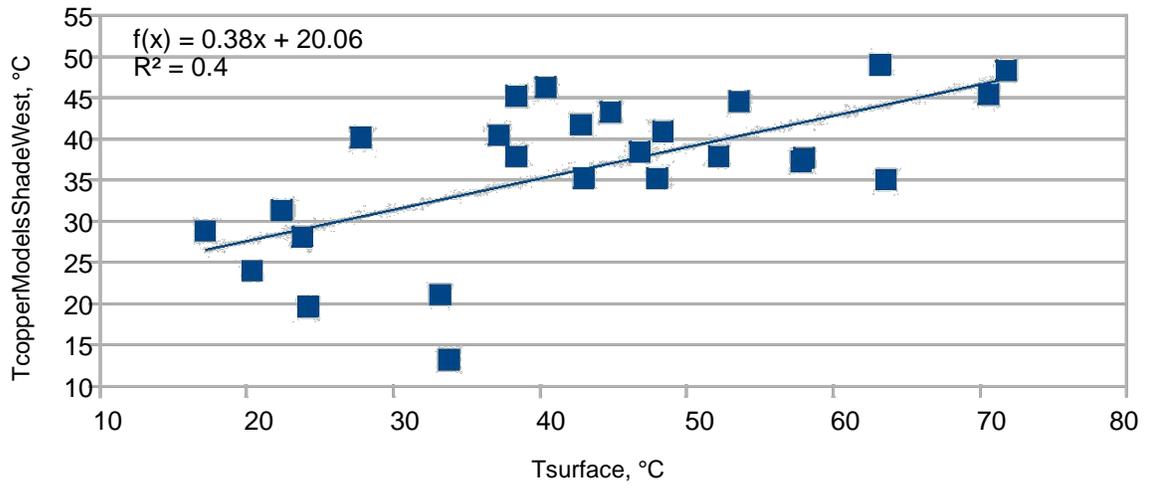






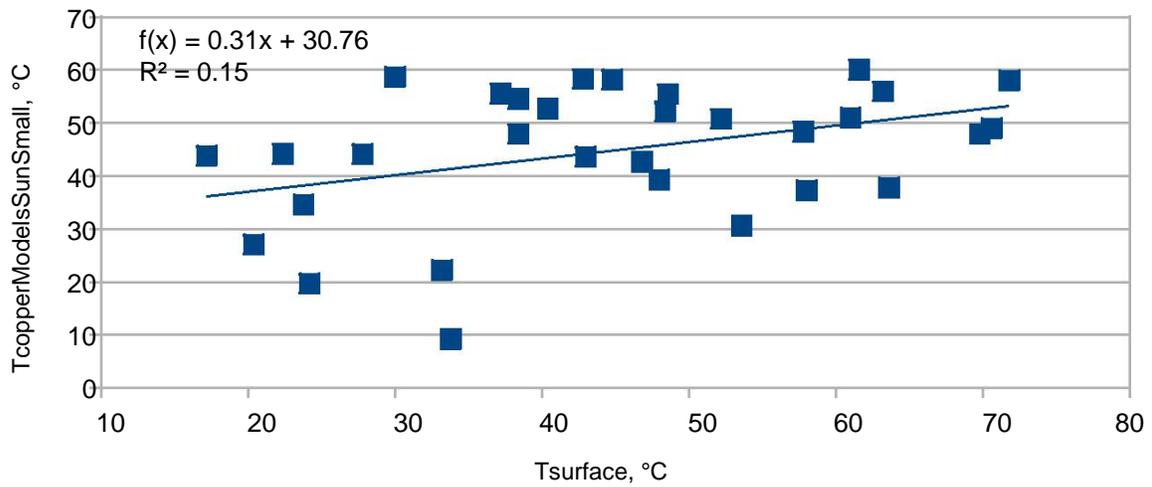
Analysis Cammy, Temperature

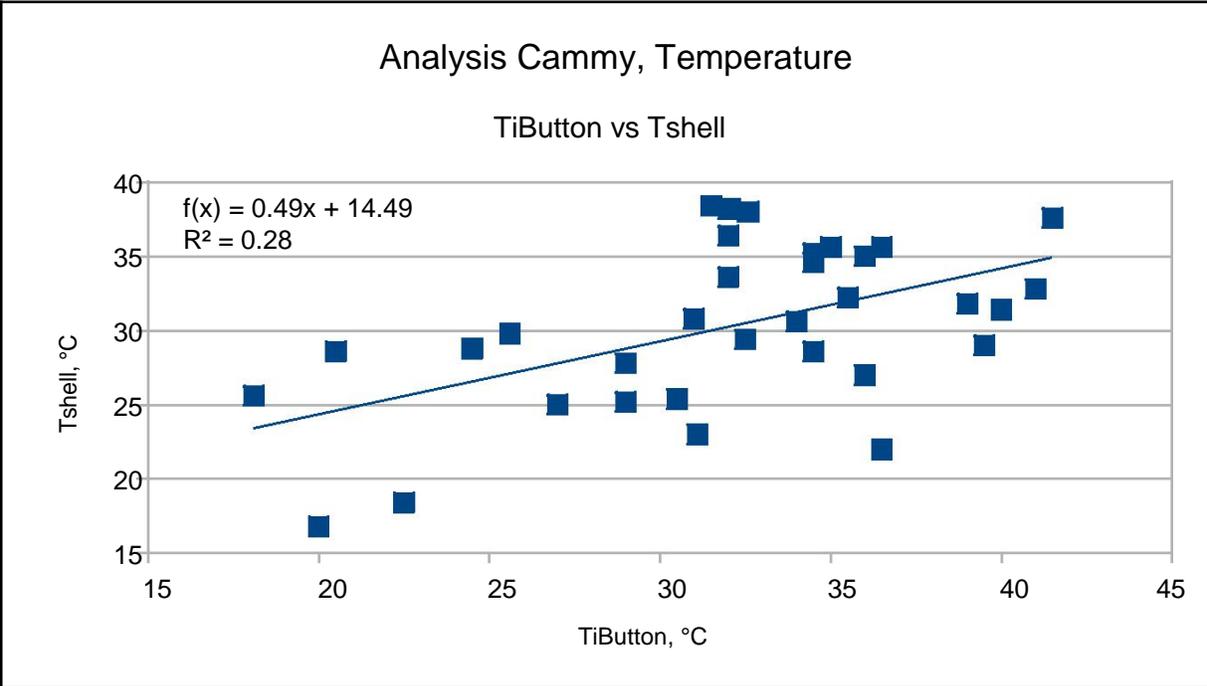
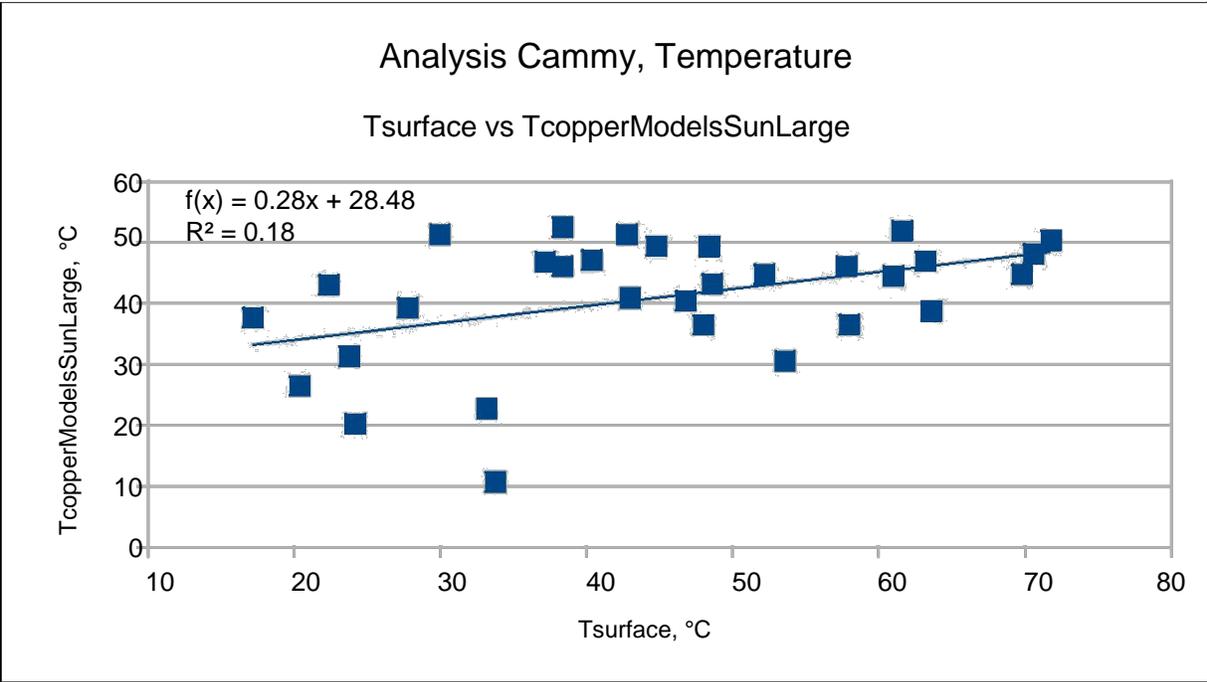
Tsurface vs TcopperModelsShadeWest



Analysis Cammy, Temperature

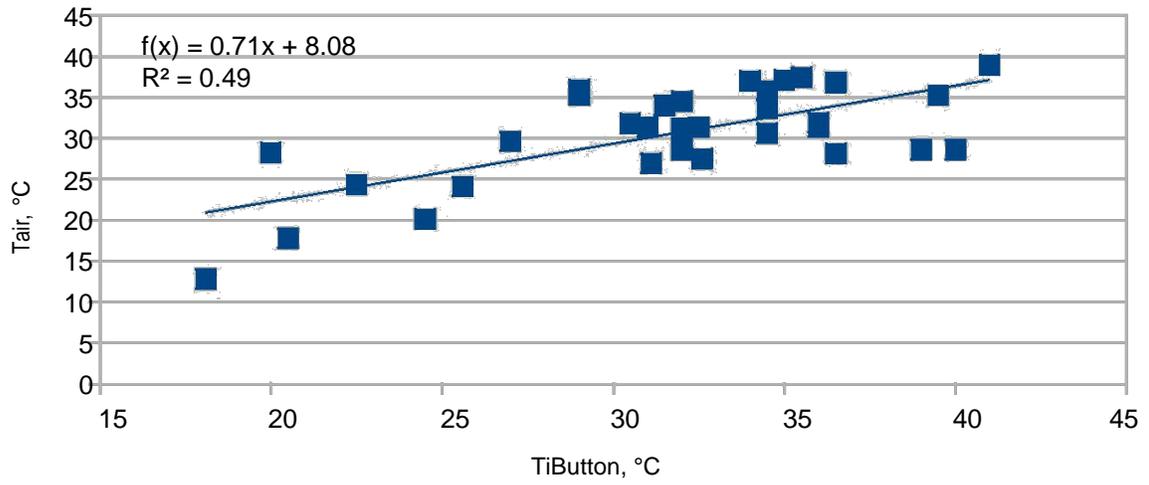
Tsurface vs TcopperModelsSunSmall





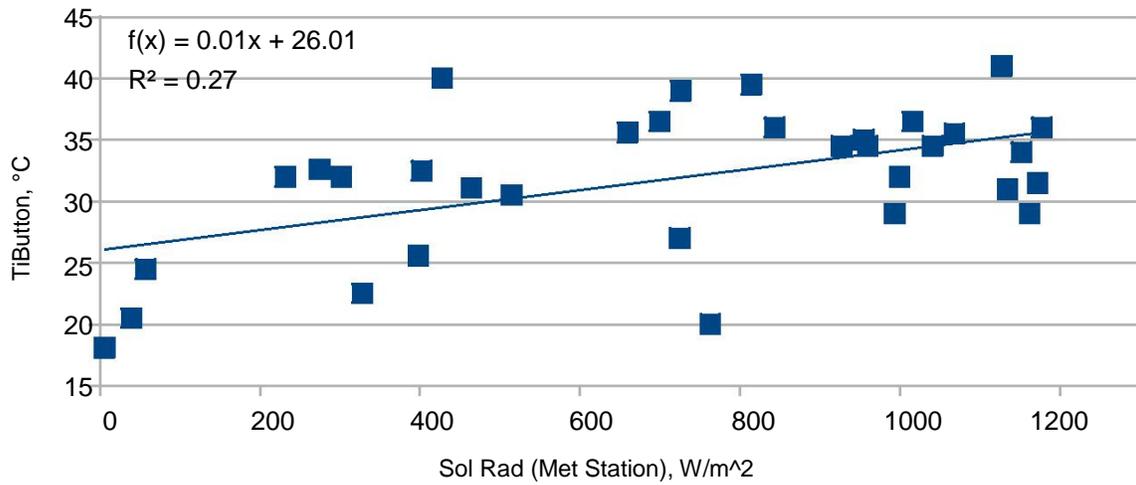
Analysis Cammy, Temperature

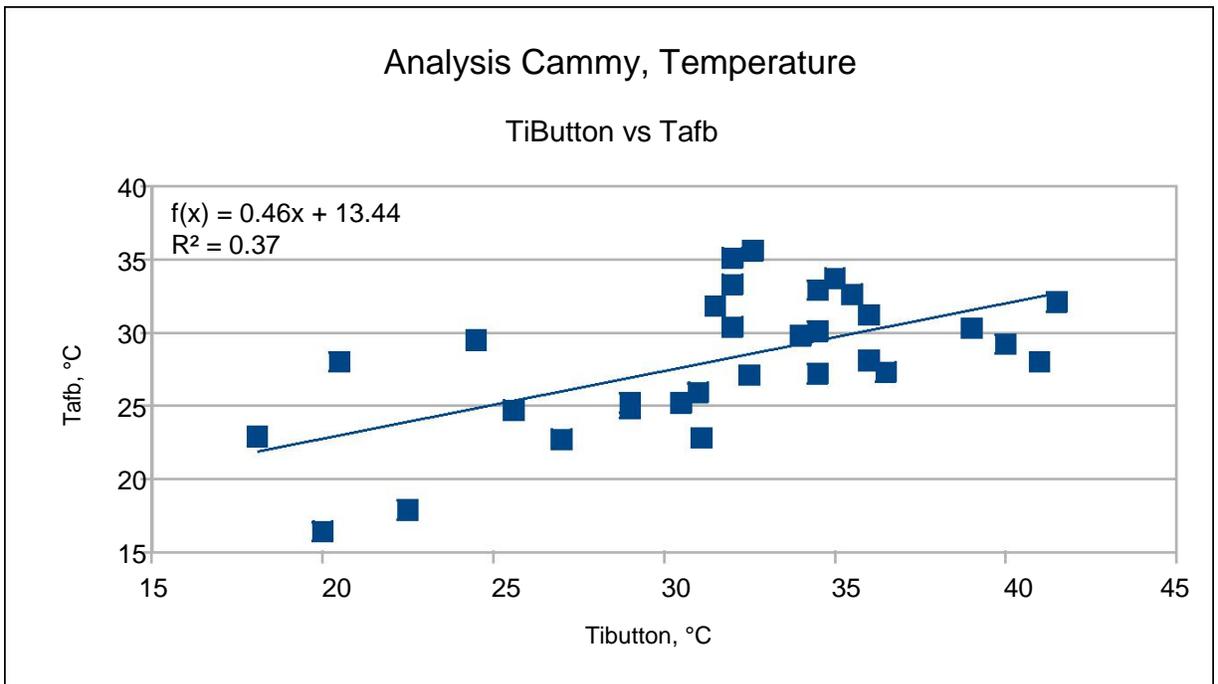
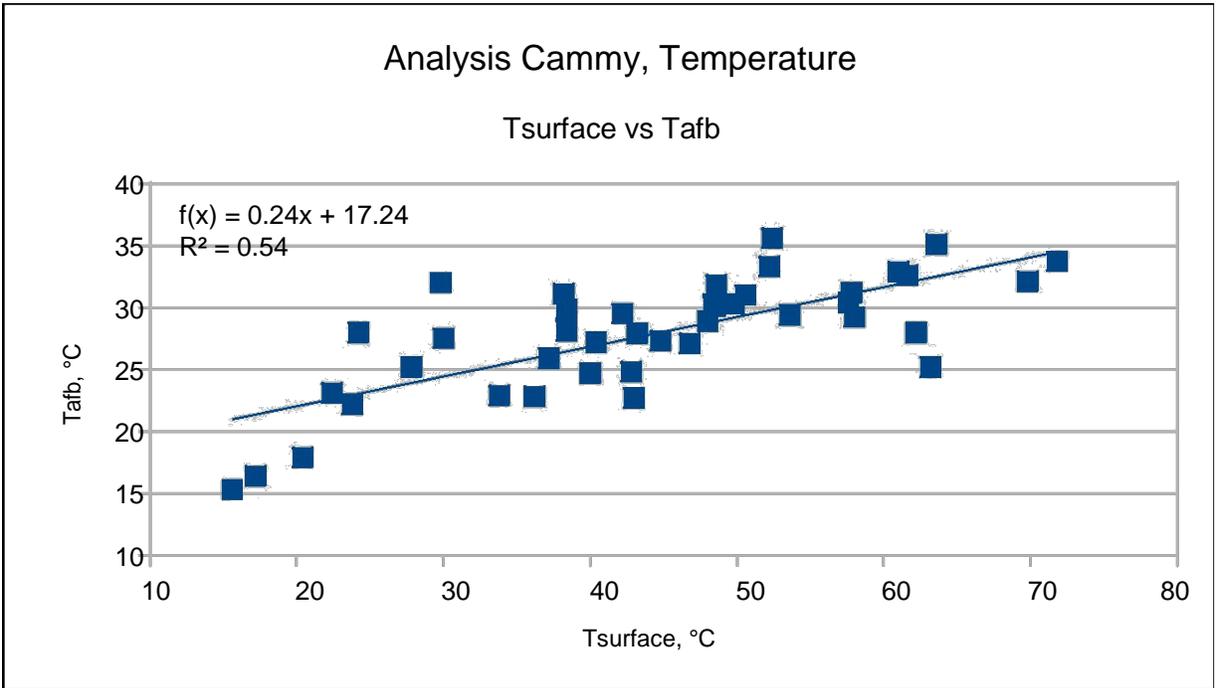
TiButton vs Tair



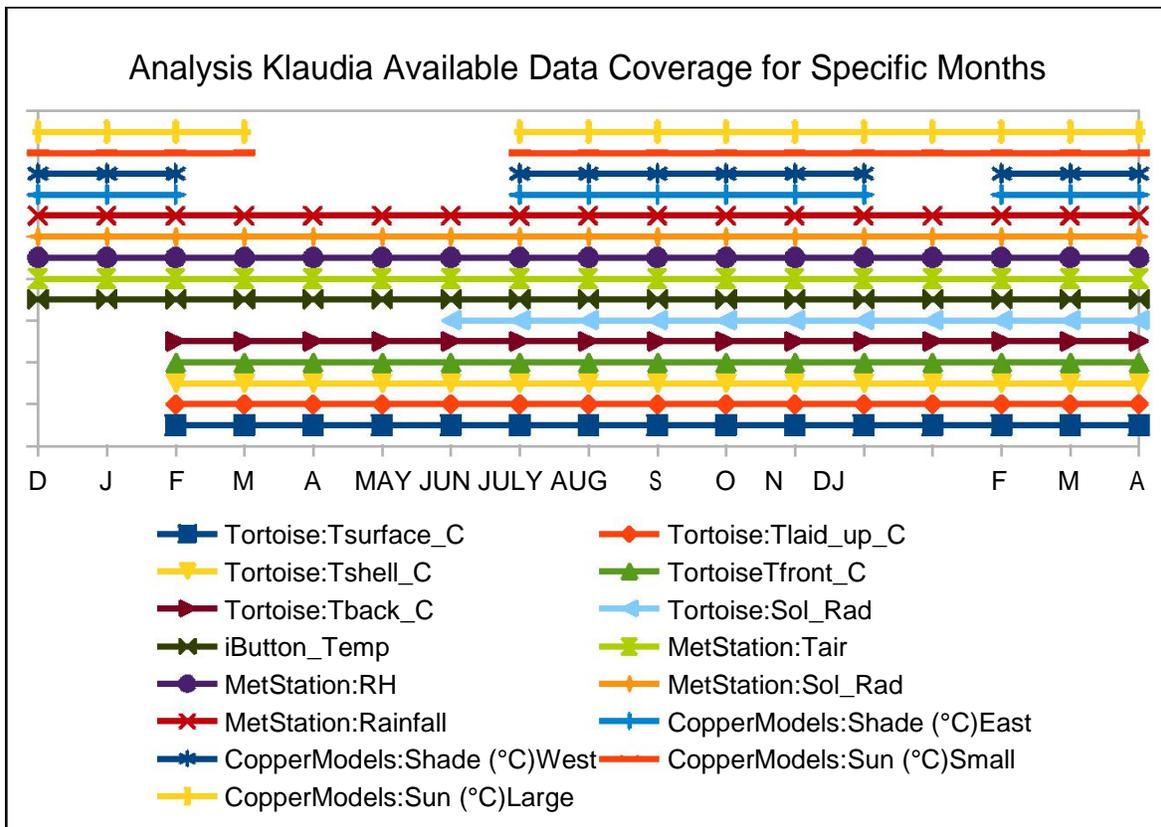
Analysis Cammy

Sol Rad (Met Station) vs TiButton



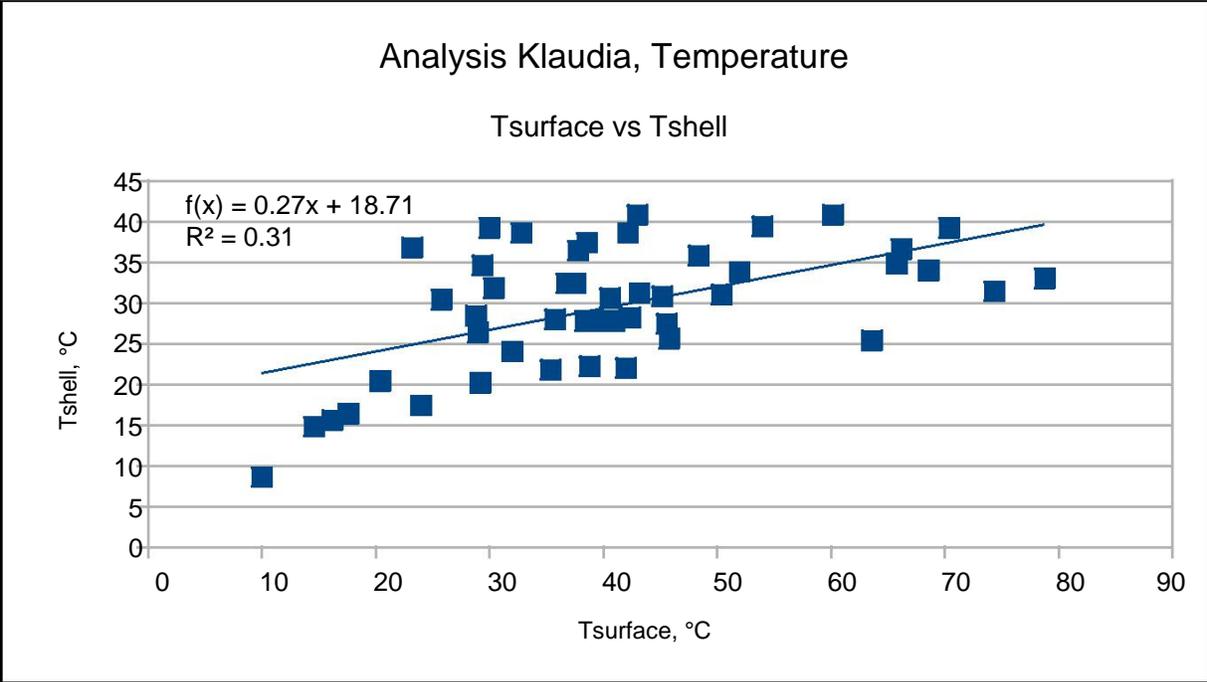
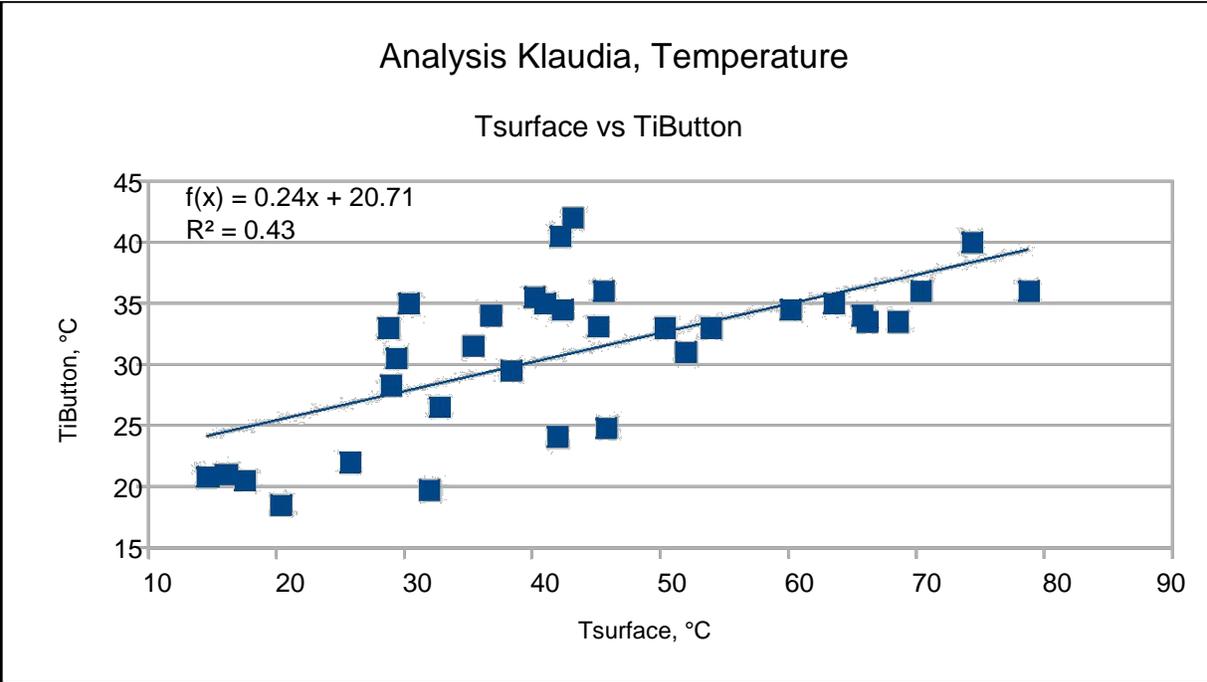


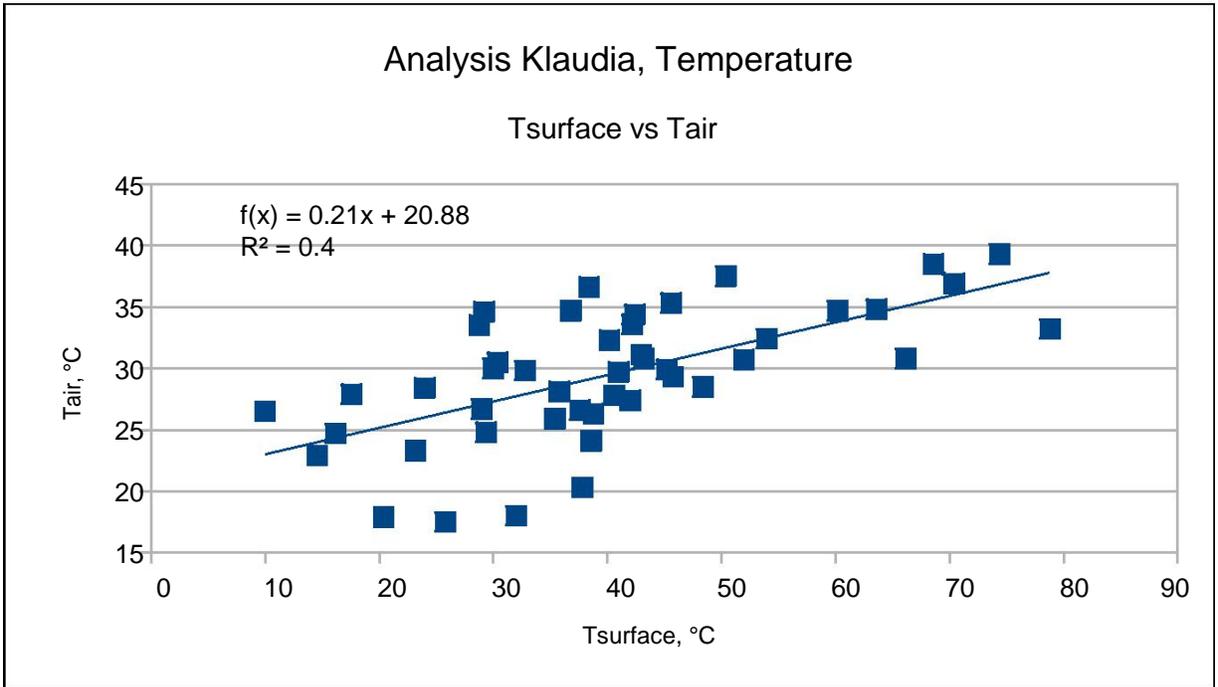
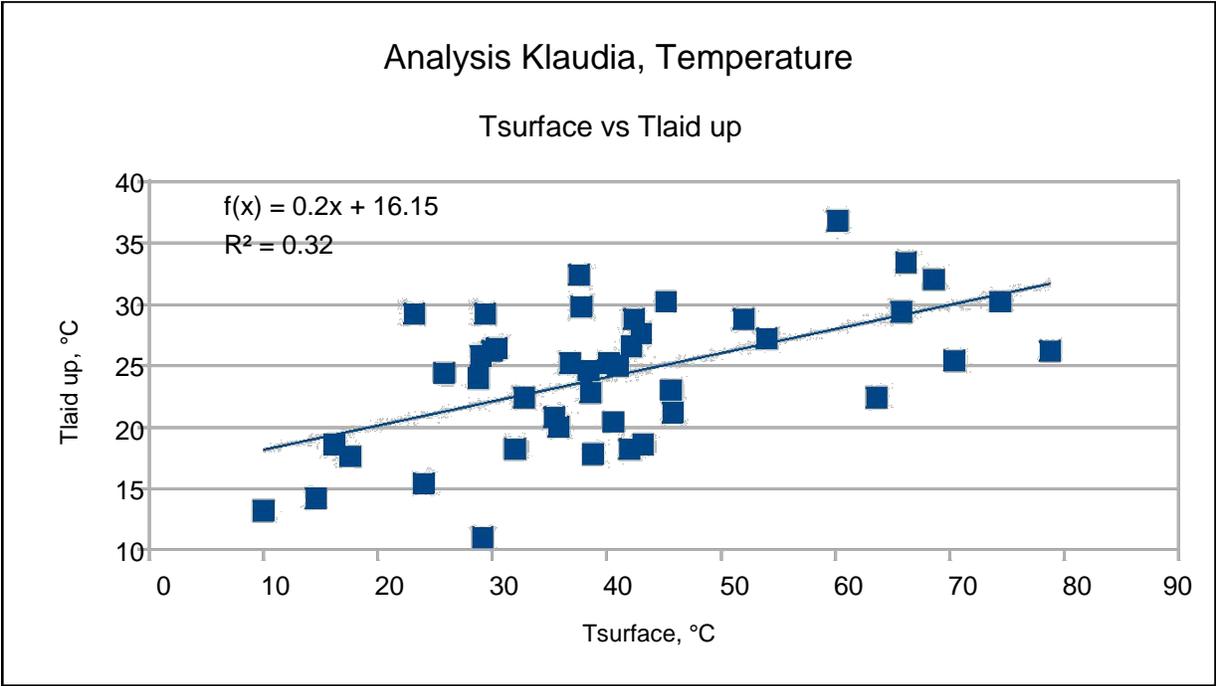
Analysis Klaudia

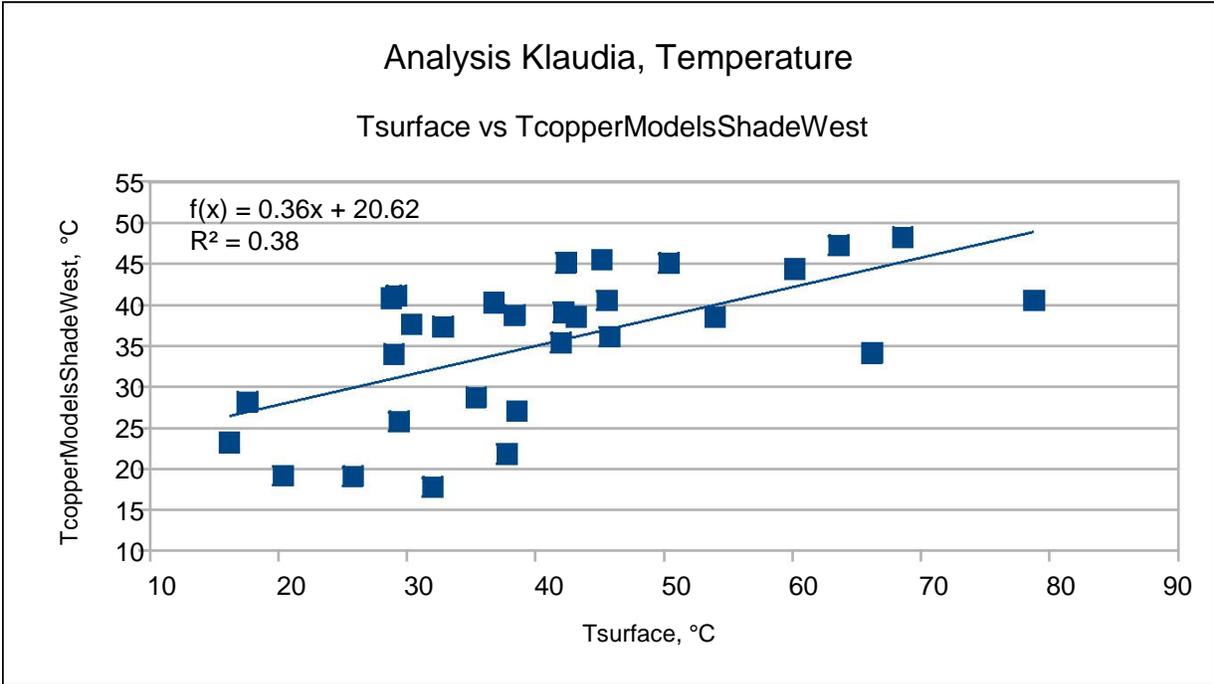
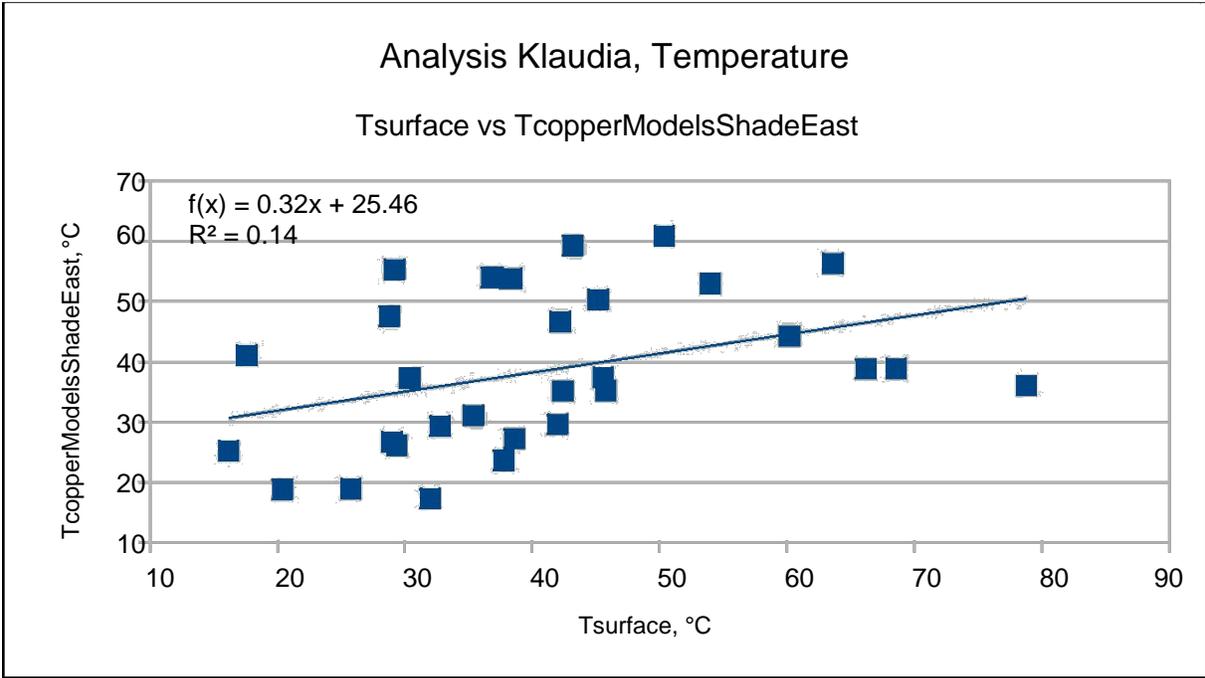


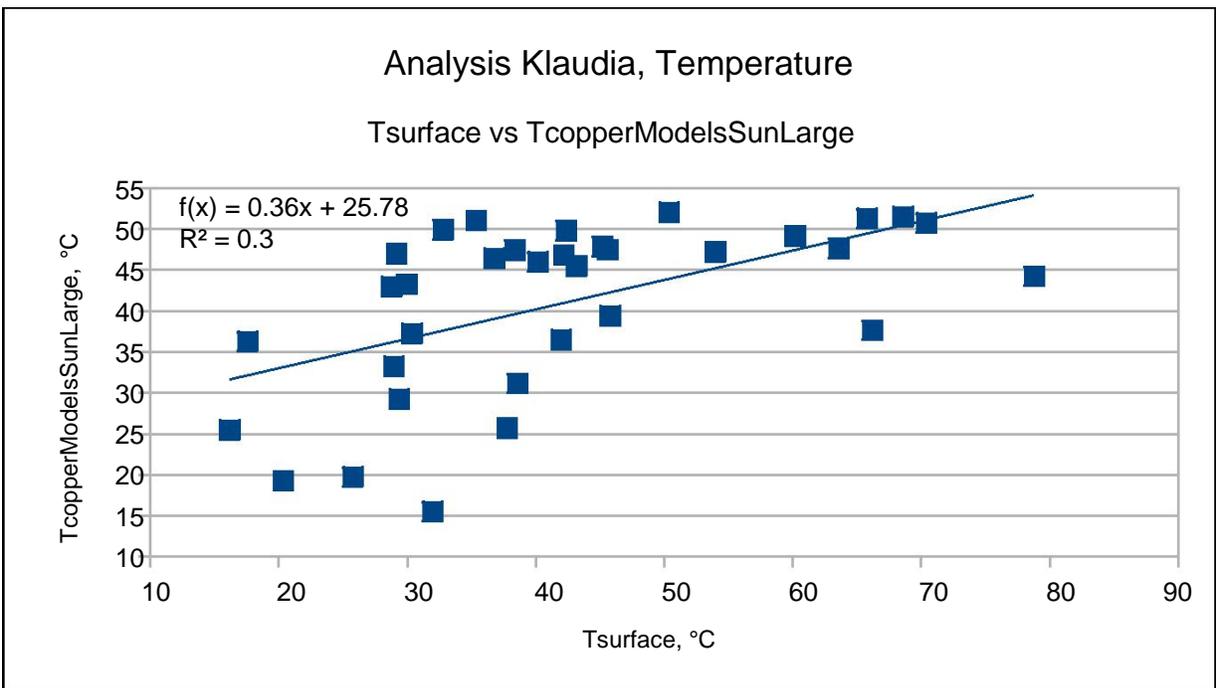
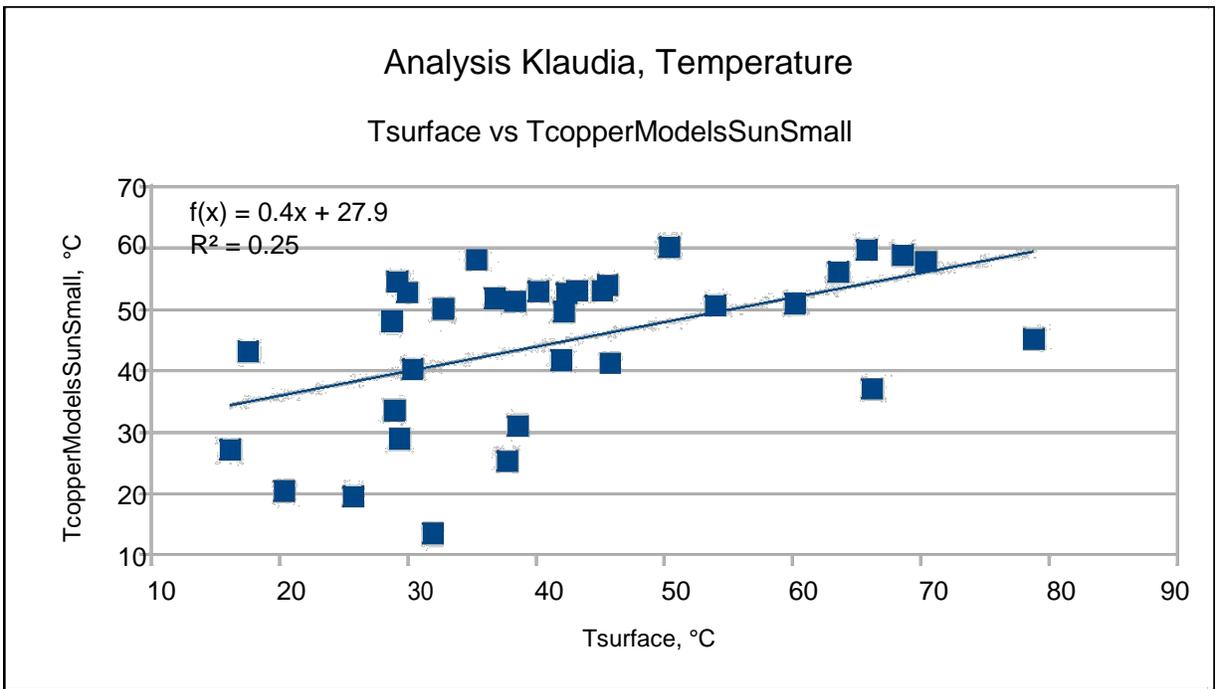
Graph File: Klaudia Analysis

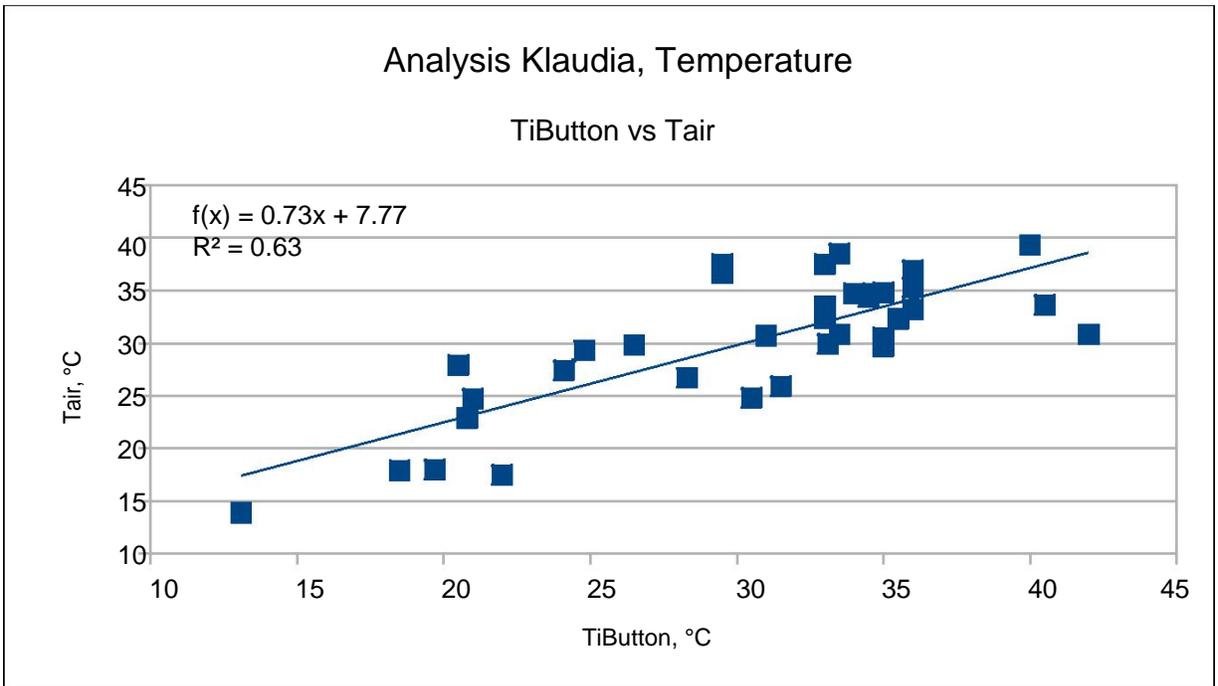
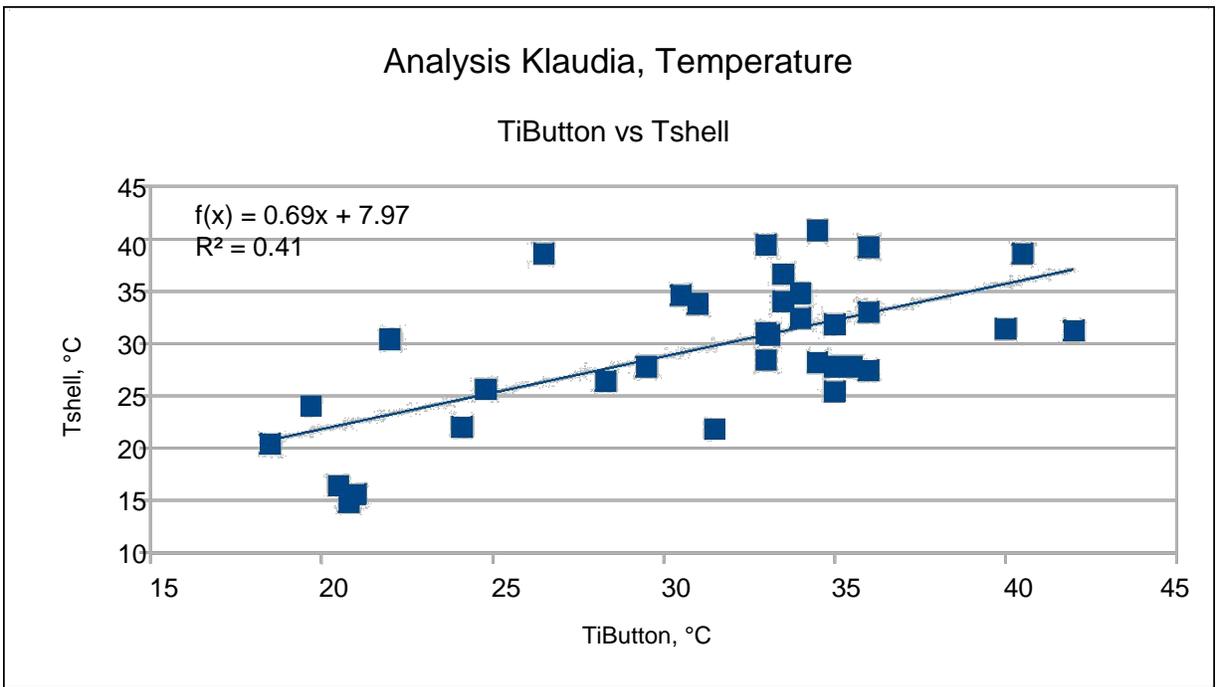
	Data Points	R ² value	Equation
1 Tsurface vs TiButton	34	0.425	$f(x) = 0.237x + 20.705$
2 Tsurface vs Tshell	47	0.313	$f(x) = 0.266x + 18.706$
3 Tsurface vs TlaidUp	44	0.319	$f(x) = 0.198x + 16.151$
4 Tsurface vs Tair	46	0.403	$f(x) = 0.215x + 20.884$
5 Tsurface vs TcopperModelsShadeEast	30	0.141	$f(x) = 0.319x + 25.465$
6 Tsurface vs TcopperModelsShadeWest	30	0.377	$f(x) = 0.359x + 20.618$
7 Tsurface vs TcopperModelsSunSmall	34	0.246	$f(x) = 0.401x + 27.9$
8 Tsurface vs TcopperModelsSunLarge	34	0.302	$f(x) = 0.359x + 25.777$
9 TiButton vs Tshell	34	0.407	$f(x) = 0.692x + 7.973$
10 TiButton vs Tair	35	0.63	$f(x) = 0.735x + 7.772$
11 SolRad vs TiButton	36	0.219	$f(x) = 0.008x + 25.180$
12 Tsurface vs Tafb	38	0.262	$f(x) = 0.203x + 17.555$
13 TiButton vs Tafb	27	0.262	$f(x) = 0.469x + 11.408$

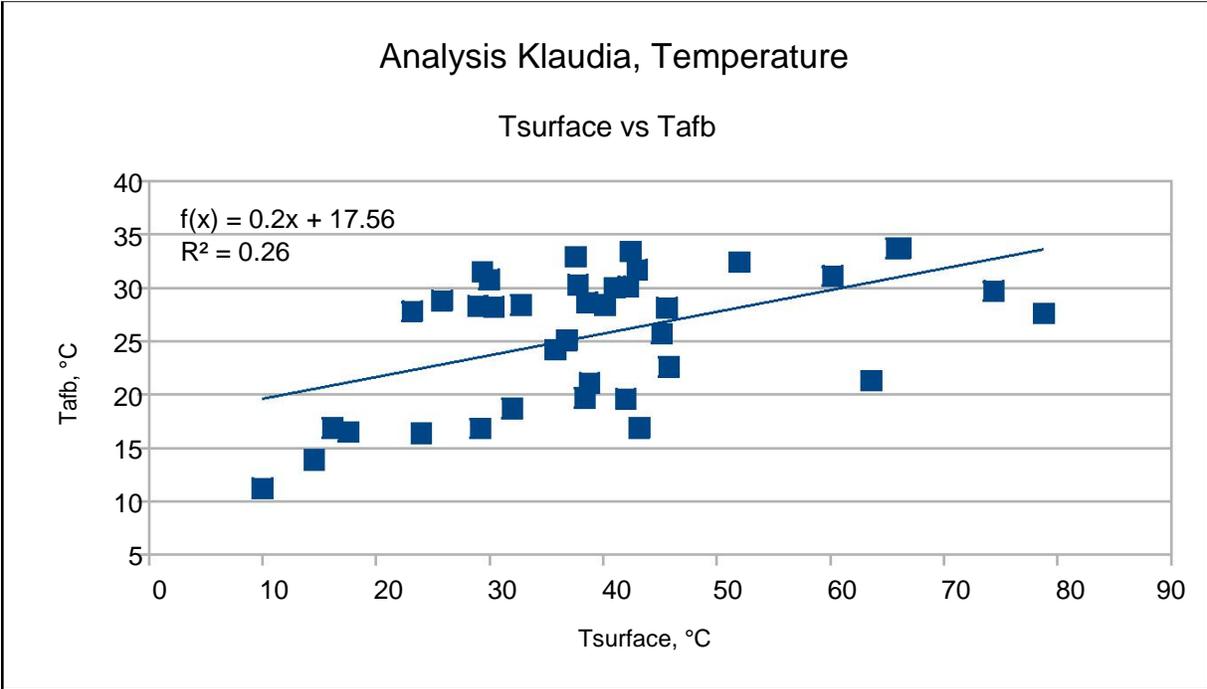
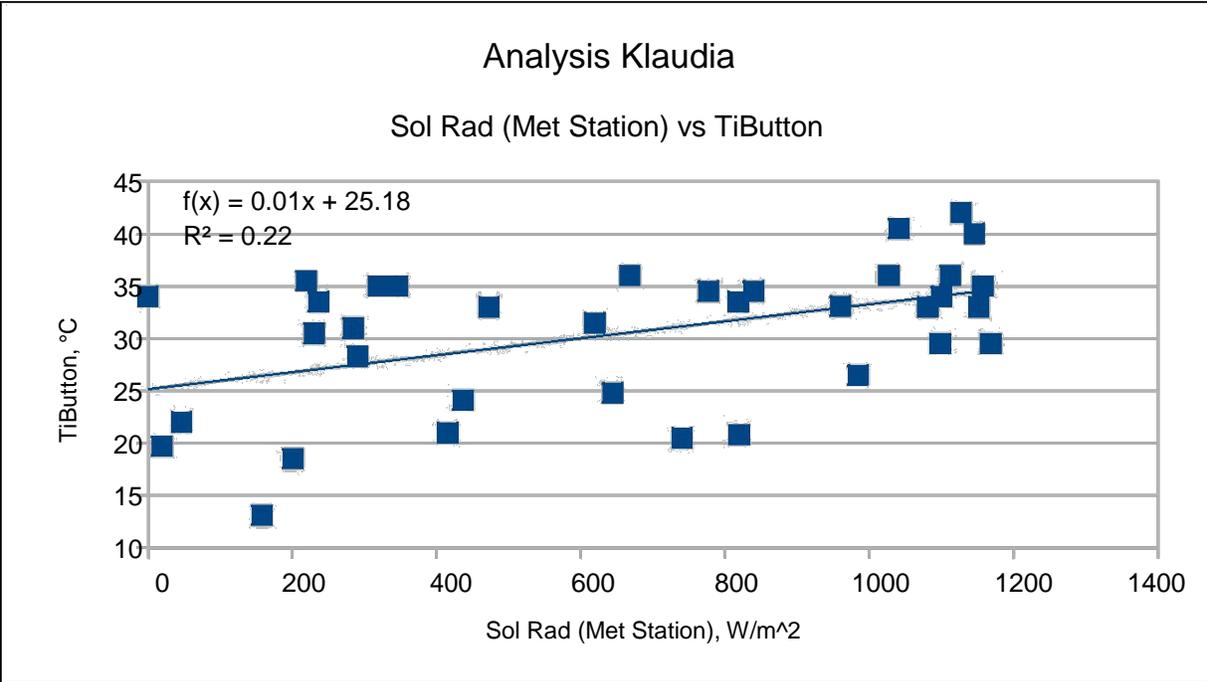


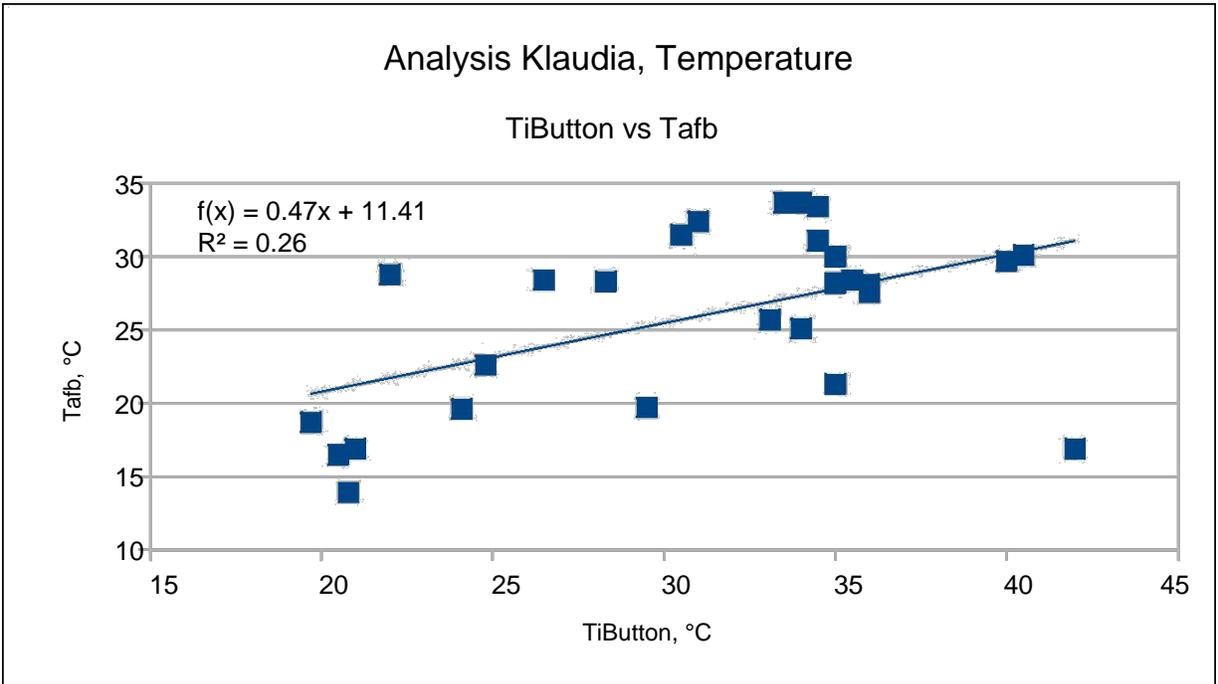








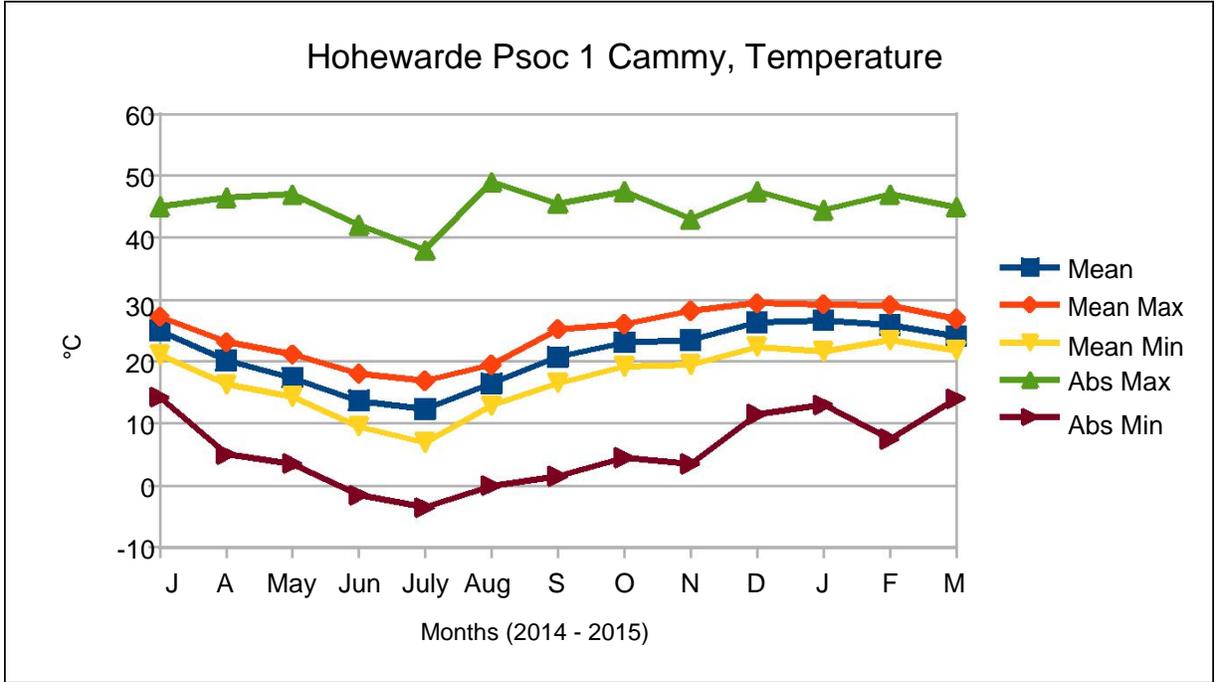




Psoc_1_Cammy_Hohewarde_20150315

Attributes within the file: Temp, °C

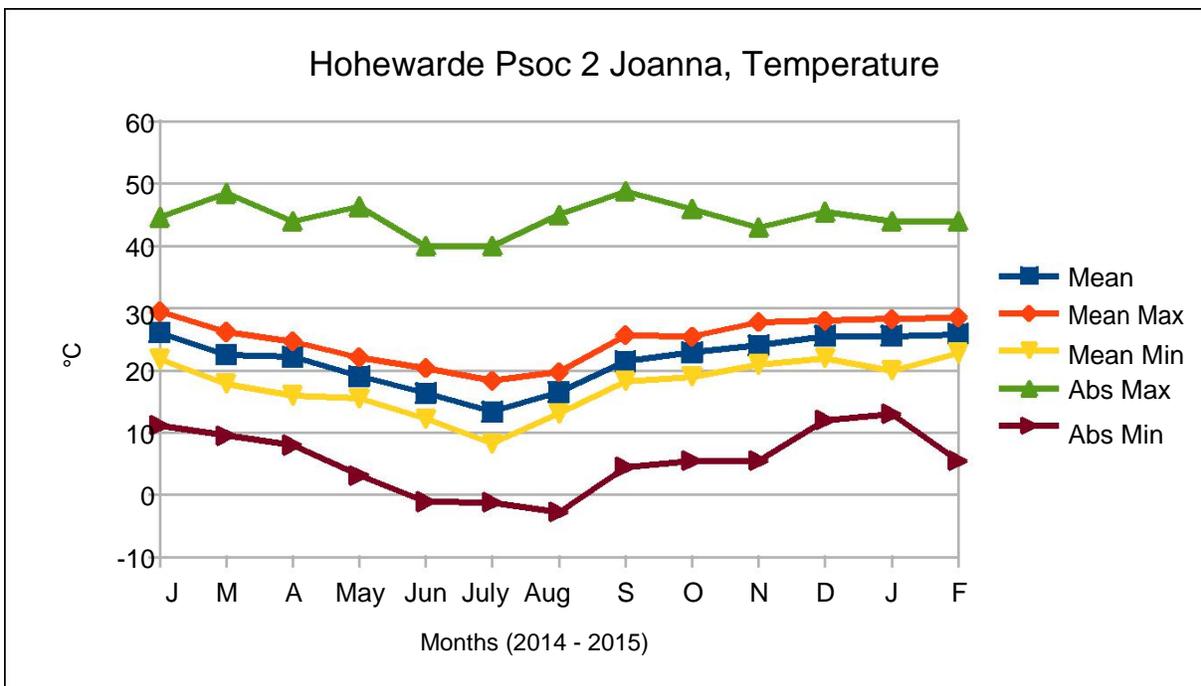
Calculated for each attribute: Monthly and daily: mean, mean max, mean min, absolute max, and absolute min



Psoc_2__Joanna_Hohewarde_20150227

Attributes within the file: Temp, °C

Calculated for each attribute: Monthly and daily: mean, mean max, mean min, absolute max, and absolute min



Hohewarte Farm Rainfall Data, December 2013-April 2015.

Year	Month	Rainfall (mm)
2013	December	97.2
2014	January	88.0
	February	123.8
	March	127.0
	April	17.7
	May	11.7
	June	0.1
	July	0.1
	August	0.0
	September	1.2
	October	2.6
	November	4.1
	December	10.9
2015	January	38.5
	February	21.5
	March	80.0
	April	5.0