# Understanding predation of tortoises by nesting Pied Crows (*Corvus albus*) in western South Africa.

Student: Carles Durà i Franch

Supervisors: Arjun Amar & Robert Thomson

Conservation Biology Master

University of Cape Town

Percy FitzPatrick Institute of African Ornithology

Private Bag X3

Rondebosch 7701

Cape Town South Africa

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## *Abstract*

Many species in a wide variety of taxonomic groups have shown shifts in their distribution ranges in recent decades. Rapidly changing distributions may lead to novel biotic interactions between species that have not historically interacted. As generalist predators, corvids are a potential threat to other species in areas where they have recently colonized or where their numbers have increased. Tortoise species appear to be one taxonomic group that may potentially suffer serious negative effects from increased corvid abundance. One species of corvid which has shown a significant range increase in the last two decades in western South Africa is the Pied Crow (*Corvus albus*). In conjunction with this expansion have come observed accounts of large numbers of tortoises being found depredated under Pied Crow nests, raising concerns over their impact on tortoises in these areas. Southern Africa has the richest biodiversity of tortoises in the world and a high rate of endemism. The endemic species are mainly restricted to the Cape region, where the genera *Chersina*, *Homopus* and *Psammobates* have their evolutionary centre. In this thesis, I explore how widespread tortoise predation by Pied Crows was during the crow's breeding season. I aimed to quantify the proportion of Pied Crow pairs that provision tortoise to their chicks and the numbers being depredated, as well as the species of tortoises involved. During the 2016 breeding season, I monitored 125 active Pied Crow nests in western South Africa. For the majority of these nests (n=93) there was no evidence for any tortoise predation. For the 32 pairs, where predation was recorded, I found that 15 pairs depredated ≤1 tortoise $^{-\text{week}}$, five pairs depredated depredated between 1 and 2 tortoise$^{-\text{week}}$ , and 12 pairs depredated >2 tortoises$^{-\text{week}}$. The tortoises prey remains found depredated depredated under Pied Crow nests had an average straight carapace length of 5.57 cm (range 3.5 cm - 9.8 cm) and 91% of them were Angulate Tortoises. Crows favour smaller tortoises with impacts for smaller species, or younger age classes. I also explored whether any environmental variables explained probability of tortoise predation or predation rates. Environmental variables examined included weather variables, land cover types, distances to roads and primary productivity values, and for a subset of nests the abundance of tortoises counted from transects. Although predation rate showed spatial variation among the study areas with most predation occurring in arid areas with high mean temperatures and low rainfall, no single environmental variable successfully predicted the variation in spatial predation.

***Key words***: Pied Crow, predation, subsidized predator, tortoise, Corvids, Angulate tortoise, *Corvus albus*.

## *Introduction*

Many species in a wide variety of taxonomic groups have shown shifts their distribution ranges in recent decades (Hickling et al. 2006). These shifts can often be explained by global environmental changes and processes including climate change, $CO_2$ enrichment, nitrogen deposition, intensification of agriculture, urbanization, reduction of spatial barriers, water availability and invasions aided by humans (Tylianakis et al. 2008). Historical data show that species undergo natural changes in their distributions, but current rates are likely more rapid and the trends in these changes are predicted to increase in the future (McCluney et al. 2012). The conservation of several species may face considerable ecological challenges due to their shifting ranges. This can lead to a high risk of extinction for affected species (MacLeod 2009).

Rapidly changing distributions may lead to novel biotic interactions between species that have not historically interacted. A well-known example is the Avian Malaria (*Plasmodium relictum*) parasite, which caused a major conservation crisis infecting several species of Hawaiian Honeycreepers (Depanidinae) when it was introduced in Hawaii. This new biotic encounter led to waves of extinction (Atkinson et al. 2014). In the past century, plant pathogens introduced from distant continents have caused large-scale transformation of native ecosystems around the world (Parker 2004). In Fennoscandia, numbers of Red Foxes (*Vulpes vulpes*) are increasing due to rising temperatures and decreased predation by wolves. In relation, Artic Foxes *(Alopex lagopus)*, which are native to Fennoscandia, are being pushed by the red foxes further north, resulting in decreases in range and population density of their area of origin (Hersteinsson et al. 1989 & Hersteinsson et al. 1990). In the Western Isles, Scotland, the American Mink (*Mustela vison*), an invasive predator, has decreased the colony size and decreased the breeding success of different species of terns (Clode et al. 2002). These novel interactions can be hugely destructive, posing difficult-to-predict outcomes and subsequently more challenging methods of control.

Predation is an interaction which may have large impacts on prey populations. Naïve prey species that lack an evolutionary history with the novel predator are susceptible to high rates of predation, and risk population decrease or even extinction (Salo et al. 2007). These types of novel interactions can also alter the food web; loss of species within high trophic levels may lead to increases of species lower down the food chain such as herbivores (Tylianakis et al. 2008). In addition, generalist predators might have more severe impacts than specialist predators due to their ability to utilize and benefit from other food sources in modified habitats. If generalist predators are good colonizers, prey species may be affected or induced on local extinctions (Rand et al 2006). Perhaps the best examples of new predator-prey relationships that have had negative effects on prey are where predator species have been introduced by humans where they were historically absent. For example, the impact of Red foxes on small marsupials in Australia (Sih et al. 2009) or the introduction of brown tree snakes (*Boiga irregularis*) on birds in Guam (Sih et al. 2009). However, the evidence of native invaders expansion has been less documented than the evidence of the exotic species impact as much of the present conservation debate focuses on alien species.

As generalist predators, corvids have the potential to be a threat to other species in areas where they have recently colonized or where their numbers have increased. Corvids are widespread, adaptable and opportunistic (Marzluff et al. 2001). They are often viewed as efficient predators that can potentially threaten the viability of other species. Many corvid species densities and ranges are increasing across the globe due to urbanization and land use changes and they are thought to be a threat for other species in areas where they have colonized recently or in the areas where their numbers have increased recently (Amar et al. 2010). For example, American Crows (*Corvus brachyrhynchos*) increased in urban areas across the USA from 1960 to 1996 with a mean annual increase rate of 27%. This species has benefitted from all year-round food sources, high immigration of non-breeding individuals, novel nesting opportunities and a huge decrease of territory size needed by breeders. In spite of the huge increase, there was no evidence that they had a large negative impact on other urban birds. Corvids were only implicated on 6.2% of egg predation and 2.0% on chick predation, out of over 900 observations on artificial nests sites (Marzluff et al. 2001). In their global review, Madden et al. (2015) found that the overall corvid impact on bird abundance was small. They concluded that bird populations were usually unlikely to be limited by corvid predation and that conservation funds should be focussed on other priorities (Madden et al. 2015). However, Madden et al (2015) recognised the biases in the studies used in their review, these include the fact that i) all studies conducted were from the northern hemisphere (no studies were found from African systems), ii) the review only considered impacts on avian populations.

One taxonomic group that appears to potentially suffer extreme negative effects of Corvids, are the tortoises. In the Mojave Desert (USA), for example, the Common Raven (*Corvus corax*) is the major predator of the Desert Tortoise (*Gopherus agassizii*). Between 1968 and 1988, Common Raven numbers increased by a 1500% (Boarman 1992). They were considered to be human subsidized predators, whereby they increase in number due to food, water or other limiting resources that increase due to human activities. This increase in raven numbers heavily impacted a population of the threatened Desert Tortoise. Notably the juvenile class of the tortoise was significantly impacted with severe decreases documented (Boarman 1992). Another example of corvid predation on tortoises is given by Perälä (2006) where Brown-necked Raven (*Corvus ruficollis*) depredated on juvenile Mediterranean Spur-thighed Tortoises (*Testudo graeca*) and the critically endangered Kleinmann's tortoise (*Testudo kleinmanni*). Brown-necked Raven was identified as one of the major threats to this tortoise (Perala 2006). Despite these examples, very little work has been done on corvid predation on tortoises elsewhere, including in southern Africa. Tortoises may generally be vulnerable to invasive predators, especially in arid environments, where the species are small and for young classes (for their smaller size or weaker defences).

Pied Crows (*Corvus albus*) have shown a significant increase in the last two decades in western South Africa (Cunningham et al. 2016). Pied Crows occur commonly throughout sub-Saharan Africa except where there is desert or tropical forest (Gwahaba 1975). They forage mainly on the ground. They are omnivorous, but they favour plant materials such as seeds. They are also eat a diverse range of animals including invertebrates (e.g. locusts, beetles, mollusc, termites) and vertebrates, including fish, lizards, tortoises, snakes, birds, bird's eggs, small mammals and carrion. They are monogamous and territorial, but sometimes nests are less than 200 meters apart. Although it's a widespread corvid in Africa, it is still unknown if they double brood (Hockey et al. 2005). Their changing distribution, mainly westwards is most likely due to climate change and facilitated by new nest sites such as power-lines. Pied Crows have already been termed a native invader (Cunningham et al. 2016). Their increase may have also been facilitated by roads, providing food from road kills (Grant et al. 2017). Grant et al. (2017) found a significant relationship between number of road kills and abundance of Pied Crows and they suggest an increase of Pied Crows around roads increases the predation pressure of the areas near roads.

In theory, a native invader may be able to cause trophic cascades, and this could currently be occurring for Pied Crows in western South Africa, where in the Karoo and fynbos ecosystems increases have been the greatest. Within South Africa, Pied Crows are known to mob, harass and compete with raptors for nesting places, and are notorious nest predators (Cunningham et al. 2016). However, the ecological impact of Pied Crows remains unknown. However, an indication of the potential impact that Pied Crows may have come from reports and predation on tortoises. Loehr 2017 suggested that the decrease of the population of speckled padlopers in South Africa could be due to Pied Crow predation of the small individuals. In 2013, at least 314 small Angulate Tortoises (*Chersina angulata*) and 1 small Common Padloper (*Homopus aerolatus*) were found under a Pied Crow nest in the Karoo (Fincham & Lambrechts 2014). This could be an isolated occurrence of predation or could be at the extreme high level of what is naturally occurring; alternatively this could represent typical levels of predation by this species. Therefore, understanding how widespread this level of tortoise predation is and thus its potential impacts on tortoise population is critical. Indeed BirdLife South Africa has stressed the urgent need for empirical evidence on this issue (BirdLife South Africa 2012).

Southern Africa has the richest biodiversity of tortoises in the world and high endemism. The endemic species are mainly restricted to the Cape region, where the genera *Chersina*, *Homopus* and *Psammobates* have their evolutionary centre (Branch et al. 1995). This area also hosts the world's rarest tortoise, the critically endangered Geometric tortoise (*Psammobates geometricus*). The tortoise species in western South Africa are rainfall dependent; they are long-lived species with low reproductive rates and, reach maturity late in life which makes them vulnerable to rapidly changing conditions (Loehr et al. 2004). Therefore, high predation pressure by Pied Crows (e.g., Fincham & Lambrechts 2014) may well be unsustainable for the tortoises in the regions where Pied Crows are increasing.

In this study, I explored how widespread predation of tortoises by Pied Crows was during the crow's breeding season, and to quantify the rates of predation (and the species depredated) by those pairs that were found to depredate tortoises. Moreover, I aimed to determine whether there is selection for certain size classes of tortoises that were depredated. Finally, I explored whether any key environmental factors influenced tortoise predation, specifically exploring whether probability of tortoise predation varied based on the location of the nest site (surrounding habitat or distance to the road) or the local weather conditions, and for a subset of nests, whether predation was simply a function of local tortoise abundance. Tortoise predation was predicted to be more likely or higher: 1) near  roads, because roadkills increase numbers of Pied Crows in the area and that can increases hyperpredation; 2) in habitat with more open vegetation thereby increasing the accessibility of tortoises to predation 3) in areas with higher tortoise abundance.

## ***Methods***

### *Nest searching*

I searched for Pied Crow nests by vehicle between the 29th of August and 9th of December of 2016, within 150km of Cape Town, in the Western Cape, South Africa. When I encountered a Pied Crow, I followed it for a maximum of half an hour to observe if it returned to a nest site. I searched in both natural and agricultural land, but avoided urban habitats. Once a nest was found I recorded the GPS location of the nest, the type of nest location and checked the nest status (active or inactive). If the nest had nestlings, I determined the brood size and the approximate age (and therefore laying date) by referencing chick age descriptions provided in Hockey et al. (2005). I also published an advertisement in a farmer's newspaper and on Facebook birding groups requesting for nest locations. In addition, I visited an area in Namaqualand because I was informed that there was predation on tortoises by nesting Pied Crows. I also received nest location and tortoise predation data at nests from collaborators working in the Northern Cape. My final data set contained nests located in the following areas: West Coast, Lambert's bay, Swartland, Ceres, Namaqualand and Northern Cape (Fig. 1). Thus, it is important to recognise that this sample of nests may not be representative of the predation rates of the population, but may be biased towards higher rates of predation, since I selectively visited some sites with known tortoise predation.

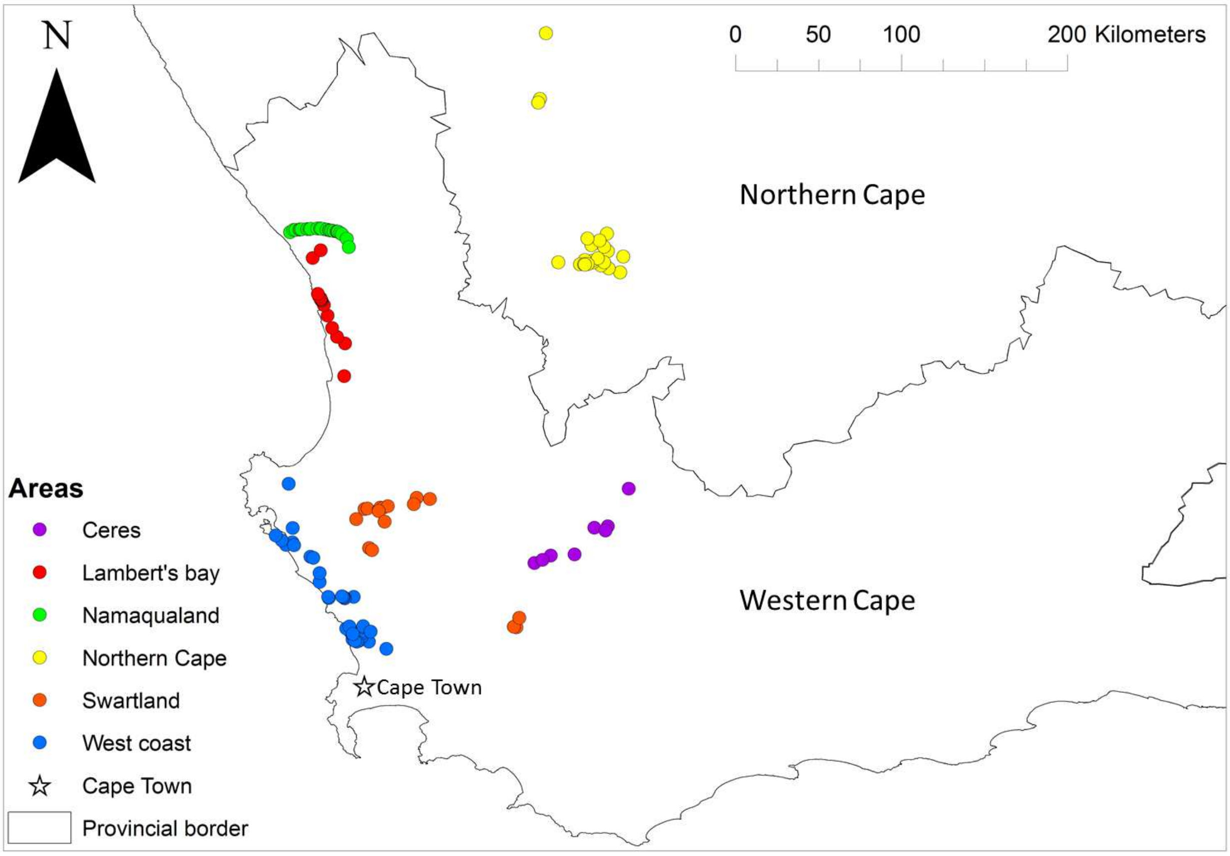

**Figure. 1. Distribution of Pied Crow nests found to be active during the 2016 breeding season western South Africa. Each colour represents a different area. This 'area' term was specified as a random factor in our analysis to control for the lack of independence between the nests in these areas.**

**Table 1. Description of the areas where active Pied Crow nests were found**

| Area | Description |
|---|---|
| **West Coast** | Southern west coast of the Western Cape with sand fynbos vegetation. |
| **Lambert's bay** | Northern west coast of the Western Cape with sand Namaqualand vegetation. More arid than the southern West Coast area. |
| **Swartland** | Agricultural areas, mostly wheat fields, including nests in the Worcester area. |
| **Ceres** | Karoo desert. Tanqua Karoo vegetation. |
| **Namaqualand** | Southern Namaqualand. All nests were on the same power-line erected two years ago. Namaqualand sand fynbos. |
| **Northern Cape** | Predominantly Hantam Karoo vegetation. Most of the nests are around Calvinia. (data collected by Rona van der Merwe) |

*Determining tortoise predation.*

Depending on the age of the chicks in a nest, I applied different methods to measure the rates of tortoise predation. First, if the chicks were less than three weeks old, all tortoise prey remains (carapaces) beneath the nest (within 30 meters radius) were cleared and collected, as some Pied Crows reuse their nest from the previous year (Hockey et al. 2005) and there might be tortoise prey remains from previous years. I then returned to these nests after 2 weeks (where possible) (Table 2) and documented and collected any new tortoise prey remains to determine the number of tortoises depredated since the last visit (surveyed time). Second, if chicks were older than three weeks, I documented all tortoise prey remains under nests (within a 30 m radius) that were fresh enough to be considered depredated during the actual season. This was done by comparison of decomposition state with carapaces found under Pied Crow nests used on previous years but not during the actual year-It wasto determine the number of tortoises preyed on since the estimated laying date until the visit date, meaning that survey time equalled the age of the chicks. No second visit was made to these nests. This was done to avoid miscalculations survey time in case chicks have fledged by the time of the second visit. Third, some nests were found after the crows' chicks had successfully fledged (clearly denoted by the condition of the nest, the amount of whitewash etc.). Again I documented the number of tortoises depredated by collecting fresh carapaces within 30 m of the nest site. This was assumed to represent the tortoises depredated throughout the full five week nestling period (Hockey et al 2005). All tortoise prey remains found below the Pied Crow nests were assumed to have been killed and depredated by the crows.

All tortoises prey remains found under and around the immediate vicinity of active nests were identified to species, and the straight carapace length was measured with a digital sliding calliper. Thus, for each monitored nest site I had information on the minimum number of tortoises depredated and the exact (or approximate) number of weeks these were produced over. These counts of tortoise prey remains represent the minimum number depredated because some tortoise prey remains may have been removed from beneath the nest site by scavengers.

To explore the extent of any underestimate in predation rates due to scavenging, I also examined the rate at which tortoise prey remains were likely to disappear. To do this I collected 51 tortoise prey remains (carapaces) from beneath a power line in West Coast National Park where Pied Crows frequent, and marked them by cutting a triangular cut on the border of the carapace using scissors. These marked carapaces were then placed under 8 different sites inside the National Park. After 15 days, I checked these sites and recorded how many of these marked tortoise prey remains were still present. Thus, using the disappearance rate from this small trial it was possible to estimate if I might have been severely underestimating the predation rates from collecting tortoise prey remains after several weeks.

### *Estimating tortoise abundance.*

To explore whether the abundance of tortoises around the nests had a strong influence of tortoise predation rates, I collected data on tortoise abundance around a sub-set of nests. For this, during the Pied Crow chick raising period (November) I conducted transects of c. 2 km at 40 randomly selected nests sites in the areas of Ceres, Namaqualand, Northern Cape and West Coast (6, 10, 10 and 14 transects, respectively). Dates were altered between sites. Transects covered at least two directions away from the nest and covered the typical or most common habitat in the area adjacent to the nest site. Transects were not straight, with directions mainly determined by logistical constraints around the nest sites. Transects were done during the peak of the daily activity for tortoises following Ramsay et al. (2002), which was around 10 am during spring and summer. During the transects the observer walked at a slow pace of approximately 2 km per hour and searched the ground in all directions. From these transects tortoise abundance was calculated as the number of tortoises found per kilometre. Any live tortoises found on the transects were recorded. Sex was recorded when possible and the straight carapace length was measured with a digital sliding calliper. From these measurements, we were also able to compare the sizes of tortoises that were depredated with the sizes of tortoises that were available around nests sites, and therefore to explore what size tortoises were being selected by crows or whether they were being depredated in proportion to the sizes available.

### *Environmental variables*

All GPS locations of nests active in 2016 were plotted on ArcMap 10.3.1. Because no information exists on the exact size of the home range of Pied Crows I used multiple buffer circles of 500 m (meters), 1000 m and 2000 m to explore the environmental variables surrounding the nest site. The minimum buffer of 500 m was chosen on after consulting published examples of the home range sizes of other crow species, but avoiding those home ranges of crows living in urban areas (Shank 1986, Baglione et al. 2005) I then generated a tabulated area table with the different buffer circles and the following different layers: Land cover data from 2014 (72 class South African national land cover dataset that categorizes South Africa into land classes at a 30 m resolution. Categories include vegetation type e.g. grassland, open bush, dense bush, and anthropogenic categories such as urban development, mean Normalized Difference Vegetation Index (NDVI) of the last 15 years. Thereafter, I performed zonal statistics to calculate the values of each layer inside each buffer circle and the percentage of the different land cover class in each buffer; (woodland with open bushes, wetlands, cultivated land, urban areas, mines, none vegetated, grassland and thicket dense bushes and plantations). I also generated a nearest distance table with the South African roads to know the nearest distance to primarily roads, secondary roads and tertiary roads.

For the land cover data I extracted information on 18 land cover classes – where these only made up a small proportion of habitat inside each buffer circle. I combined them with other sensible groups – this produced a total of nine land cover variables (woodland with open bushes, wetlands, cultivated land, urban areas, mines, none vegetated, grassland, thicket dense bushes and plantations). To further reduce the number variables examined in our final models and to cope with many of these variables being correlated with one another, I undertook a Canonical Correspondence Analysis (CCA) which produced 4 axes describing land cover around the nest sites (CCA1, CCA2, CCA3, CCA4).

*Statistical analysis.*

All data were analysed in R v.3.2.5 (R Core Team 2013).

My main analysis explored whether any environmental variables were useful in explaining either the probability of tortoise predation or tortoise predation rates. Before running any models I first ensured none of my potential explanatory variables were correlated with each other.

I used Generalized Linear Mixed Models (GLMMs) in all analyses, with ‘study area’ specified as a random term, this was to account of the lack of independence between nests in the same areas. I first analysed whether any variables were associated with the probability that tortoise predation occurred at a nest site. Thus, for this analysis my response was binary either 1= tortoise predation occur or 2= no predation occurred. For this analysis I also fitted the number of weeks the nest was monitored for as an offset in the model. GLMMs were fitted with binomial error structure and a logit link function. Ten environmental variables were entered into the model (CCA1, CCA2, CCA3, CCA4, distance to primary roads, distance to secondary roads, distance to tertiary roads, mean day temperature, average rainfall, mean monthly NDVI over the last 15 years (2000-2015). All possible combinations of these terms were run as main effect in models. This model was repeated it for all buffer circle sizes (e.g. 500 m, 1000 m and 2000 m).

This exact same model was then repeated to explore whether any variables explained tortoise predation rates. However, for this model, I log (+1) transformed the number of prey remains (carapaces) found and fitted the model with a Gaussian distribution and an identity link function, together with an offset which was the number of weeks the nests were monitored for.

To determine which environmental variables explained either the probability of tortoise predation or predation rates, I performed model selection using Akaike's Information Criterion (AIC) and multi-model inferences with the MuMIn v.1.15.6 package (Barton 2016). For each analysis and for each buffer circle size, I ranked the models using their corrected $AIC_c$ values and derived the Akaike weight of each model ($W_i$), in accordance with Burnham and Anderson (2002). Model suitability was assessed using AIC ranks and model weights (Whittingham et al. 2006, Lukacs et al. 2007), where the models with the lowest $AIC_c$ value and highest weight were more important relative to the others. I determinated the change in AICc relative to the optimal model ($\Delta_i$), and considered plausible models all the models with $\Delta_i < 2$. I assessed the relative importance of our different environmental variables by summing the $W_i$ of each model in which the variable appeared for all plausible models ($\Delta_i < 2$). I also used this model subset to generate parameter estimates and their 95% confidence limits through model averaging.

Lastly, to explore whether tortoise abundance was a useful variable explaining the probability or rate of tortoise predation, I reran the models with a subset of the nest sites, for which I also had data on local tortoise abundance from transects conducted around the nests. For these models, I included a more limited number of additional co-variates, beside tortoise abundance (number counter per km transect). These additional co-variates were those that were identified as having the highest relative importance scores from the previous models ran on the complete dataset (see results). This model was run with the simpler structure because data from only 30 nests was in this subset of the data.

## *Results*

Means are presented ± 1 S.D.

### *Nest monitoring*

A total of 203 Pied Crow nests were found in our seven areas (Table 2). Of these 203 nests, 80 were found on metal electrical pylons (39%), 66 were on telephone or electrical poles (33%), 38 were in exotic trees (19%), 15 were in windmills (7%), 2 were in bushes (1%) and 2 were in other artificial structures (1%). I obtained data on tortoise predation rates from only the 125 nests that were active with nestlings in 2016. Pied Crow nests had an average of 2.1 (± 0.8, range 1-3, N=28) chicks per nest. From the size of the chicks most eggs were laid in September (range August-November) (Fig. 2 and Table 2).

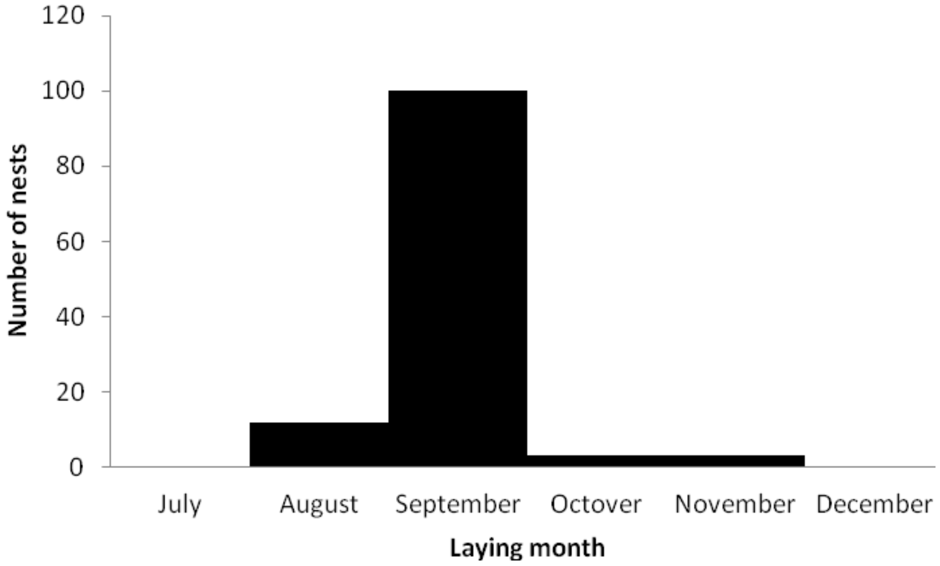

**Figure 2. Estimated month of the day of egg laying of Pied Crow nests (n=119) studied in western South Africa. Laying month was estimated either from observation of incubation and/or subsequent hatching behaviour, or where nests were found with chicks the laying month was back dated based on the approximate age of the chicks based on Hockey et al. (2005).**

*Tortoise predation levels and possibility of underestimates*

Of the 51 tortoise prey remains placed at eight poles along a power-line in West Coast National Park, 46 remained two weeks later. Therefore, 10% (5 out of 51) of tortoise prey remains were scavenged in a 15 days period. This suggested that our estimates of predation rates were not greatly underestimates, although we made no specific attempt to control for these potential underestimates in our results.

Evidence of tortoise predation was found at 32  of the 125 monitored nests (25.6%), including a total of 268 tortoise prey remains across these 32 nests. Tortoise predation varied spatially, with 65% of the tortoise prey remains found at nests in the Namaqualand area and 25% at the Northern Cape area. Throughout the rest of my study area very little tortoise predation was detected (Table 2). Although most of the monitored nests were located within the West Coast area very little predation was found there, with only one nest having one tortoise prey remains.

The surveyed period for each of the monitored nests covered the majority of the nestling period (mean of 3.9 weeks, range of 2 to 5 weeks). In Namaqualand, we found the highest rates of tortoise predation, with an average of more than $2^{-week}$ (2.23), nests in the Northern Cape area and Ceres area had a mean predation rate of $0.583^{-week}$ and $0.575^{-week}$ respectively. Mean rates of tortoise predation were negligible in other areas (Table 2).

I found no evidence for any tortoise predation at 93 of the 125 monitored Pied Crow nests. I found that 15 pairs depredated 1 or fewer tortoises per week, 5 pairs depredated 1 or 2 tortoises per week and only 12 pairs depredated more than 2 tortoises per week (Fig. 3). Thus predation was aggregated among the nest sites, with the majority of the predation occurring among relatively few nests, the distribution of tortoise predation rate therefore most closely matched an over dispersed Poisson or negative binomial distribution. Most of the 268 tortoise prey remains were Angulate Tortoises (*Chersina angulata*) (n=244; 91.0%) but I also found 23 Tent Tortoises (*Psammobates tentorius)* (8.6%) in the Northern Cape (*P. t. verroxii*) and Ceres areas (*P. t. tentorius*) and 1 Speckled Padloper (*Homopus signatus*) (0.4%) in the Northern Cape area.

**Table 2 Descriptive results of tortoise predation found under Pied Crow nests in different areas of western South Africa. Laying month was estimated with chick grown state. Nests were considered active if Pied Crows had nestlings during 2016.**

| Area | Active nests | Mean of number of chicks (N) | Laying date (month) | Mean number of weeks surveyed* | Total tortoise prey remains | Mean tortoise prey remains (range) | Mean tortoises depredated/ week |
|---|---|---|---|---|---|---|---|
| **West Coast** | 37 | 2.7±0.76 (7) | 9.00 | 3.8 | 1 | 0.02±0.16 (0-1) | 0.007±0.04 |
| **Swartland** | 17 | 2.0 (1) | 8.79 | 3.8 | 0 | 0±0 | 0.000 |
| **Lambert's bay** | 14 | 1.9±0.69 (7) | 8.80 | 5.0 | 0 | 0±0 | 0.000 |
| **Namaqualand** | 25 | 1.5±0.75 (7) | 8.88 | 3.0 | 175 | 7.00±7.11 (0-23) | 2.333±2.37 |
| **Ceres** | 8 | 1.3 ±0.57 (3) | 8.70 | 5.0 | 23 | 2.87±4.82 (0-12) | 0.575±0.96 |
| **Northern Cape** | 24 | 2.6±0.58 (3) | 9.25 | 4.9 | 69 | 2.88±8.50 (0-34) | 0.583±0.701 |
| **Total** | **125** | **2.1±0.81** | **8.90** | **4.0** | **268** | **2.14± 5.65** | **0.617±1.57** |

*Period of time between visits to collect tortoise prey remains, (5 if collection occurred after fledging representing the entire chick rearing duration (Hockey et al. 2005).

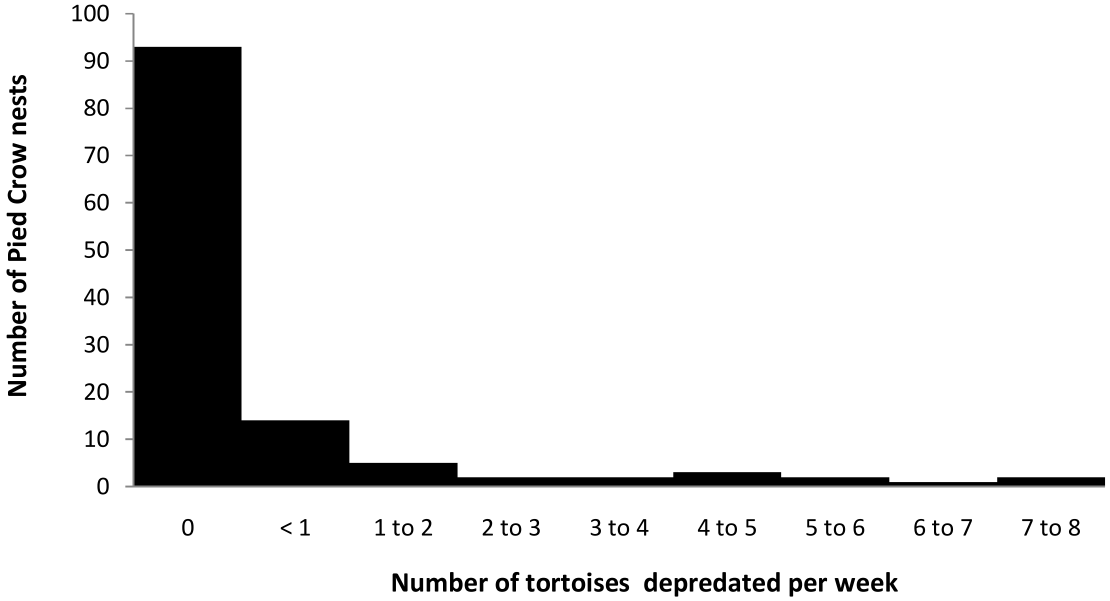

**Figure 3. Frequency histogram showing predation rates (number per week) of tortoises Pied Crows based on the number of tortoise carapaces found under nests in western South Africa accounting for the length of the activity at the nest between prey searches.**

### *Predated tortoise size classes*

Predated tortoises found under Pied Crow nest had an average straight carapace length of 5.57 cm (range 3.5 cm - 9.8 cm; n = 251). For Angulate tortoises, the mean was 5.5 cm (range of 3.5 - 7.4 cm; n = 227; Fig. 4), for Tent Tortoises 5.68 cm (range of 3.60 cm – 9.80 cm; n = 23) and single Speckled Padloper was 6.0 cm. The straight carapace lengths of all tortoises found alive during transects were larger than those of the tortoises that the Pied Crows were predating with only one exception. Straight carapace length of Angulate Tortoises found on transects had a mean of 15.85 cm (ranged 5.4 - 21 cm; Fig. 4). Thus, it was quite clear that Pied Crows were actively predating only a subsection of the different sizes of tortoises available, rather than predating tortoises by size according to their availability. I was able to sex 41 Angulate tortoises, from these, 33 tortoises were male and 8 were female.

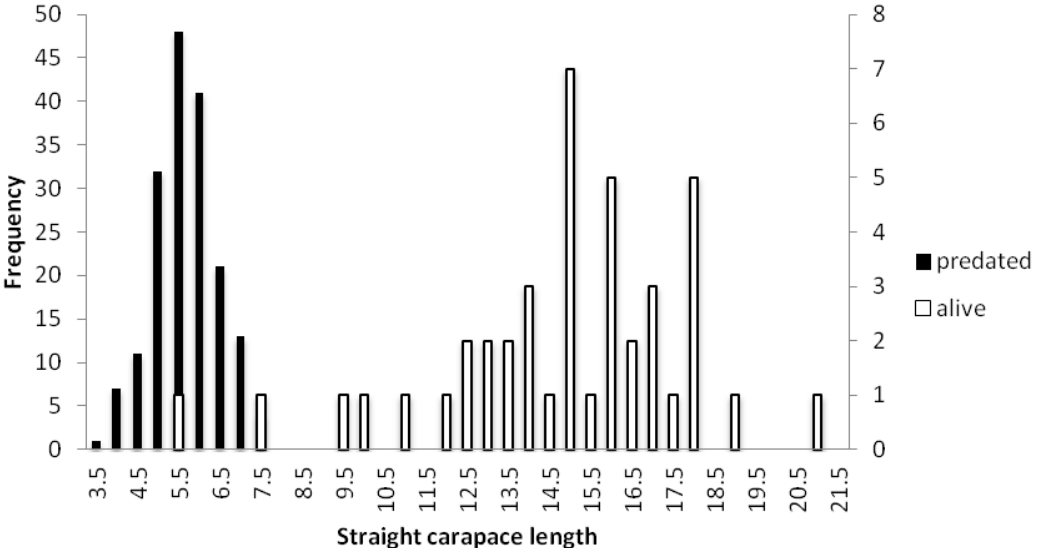

**Figure 4. Frequency of straight carapaces length of Angulate Tortoises found in western South Africa. The black bars represent the carapaces found depredated under Pied Crow nests on the left axis and the white bars represent the tortoises found alive during transects around Pied Crow nests on the right axis.**

*Environmental factors and tortoise predation rates*

The CCA performed to reduce the number of environmental variables, produced four CCA axes that explained a total of 79% of the variation in the 500 meters buffer, 84% in the 1000 meters buffer and 88% in the 2000 meters buffer. These CCA variables explained independent aspects of environmental aspects found in the study; details of the loading of the CCA variables are explained in Table 3.

In total transects to count tortoises were completed around 40 monitored crow nests; 14 in West Coast, 10 in Namaqualand, 10 in the Northern Cape area and 6 in Ceres. An average of 0.56±1.12 tortoises were found per kilometre across all transects; 1.07±1.55 in West Coast, 0.65±1.03 in Namaqualand, 0.16±0.26 in Ceres and 0 in the Northern Cape area. Two of these tortoises found were Leopard Tortoises, which were both found in West Coast and were most likely introduced, and all the other 43 tortoises found during transects were Angulate Tortoises.

Exploring the probability of tortoise predation occurring at a nest site, I found little evidence for one top model with 11 different plausible models for the 500 meters buffer, 7 for the 1000 meters buffer and 13 for the 2000 meters buffer (Appendix 1, A – C). Model averaging indicated consistently that only mean day temperature and average rainfall had the highest relative importance score (between 0.74-0.88) (Appendix 3, A - C) indicating a a higher predation rate in areas where mean day temperature was higher and average rainfall was lower. However, for both these terms the model averaged parameter estimates overlapped zero suggesting relatively poor predictive power (Appendix 3, A - C). The additional analysis including tortoise abundance on a subset of data provided little evidence to support the idea that probability of tortoise predation was associated with the local abundance of tortoises around the nest sites (Appendix 2), with none of the plausible models containing this variable (Appendix 4).

From the model used to explore the factors explaining the predation rates at Pied Crow nests I found even less evidence of a top model, with a very large number of plausible models for all buffer circles sizes. I found 47 different plausible models for the 500 meter buffer, 48 for the 1000 meters buffer and 22 for the 200 meters buffer (Appendix 5). Again only mean day temperature and average rainfall had a high relative important score (between 0.57-1.0) (Appendix 7). However, as with the probability of predation, for both these terms the model averaged parameter estimates overlapped zero suggesting relatively poor predictive power (Appendix 7). Similarly, the analysis exploring whether predation rate was associated with the local abundance of tortoises around the nest sites provide very little support for this, with the model averaged parameter estimates of the tortoise abundance variable overlapping zero and having a relatively low importance score (0.46) (Appendix 7).

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**Table 3. Major loads of each axis produced during the CCA and the percentage of variation that they explain per each distance buffer around the Pied Crow nests**

| | 500 meters buffer | | | 1000 meters buffer | | | 2000 meters buffer | | |
|---|---|---|---|---|---|---|---|---|---|
| | **Loaded positively** | **Loaded negatively** | **Percentage of variation explained** | **Loaded positively** | **Loaded negatively** | **Percentage of variation explained** | **Loaded positively** | **Loaded negatively** | **Percentage of variation explained** |
| **CCA1** | Cultivated land | Mines | 27% | Mines | Cultivated land | 28% | Cultivated land | Bare, none vegetated | 42% |
| **CCA2** | cultivated land | Woodland with open bushes | 22% | Bare, none vegetated | Mines | 26% | Bare, none vegetated | Woodland with open bushes | 25% |
| **CCA3** | Bare, none vegetated | Bare, none vegetated | 17% | Woodland with open bushes | Bare, none cultivated | 17% | Urban areas | Woodland with open bushes | 15% |
| **CCA4** | Urban areas | Woodland with open bushes | 13% | Woodland with open bushes | Urban areas | 13% | Scrubland | Urban areas | 6% |

## *Discussion*

This study confirmed that Pied Crows do depredate tortoises during breeding, but I found that this predation was spatially clumped in certain areas. Only a very few Pied Crow pairs were found to be predating large numbers of tortoises, whereas at the majority of nests no tortoise remains were found. My data suggest that tortoise predation rates are very rarely as high as was documented at the nest that Fincham & Lambrechts (2014) found.

The spatial variation in the predation rate suggests that Pied Crow predation on tortoises occurs more frequently in arid areas. All tortoise predation was found in Namaqualand, Northern Cape and Ceres, with the majority of predation occurring in the first two. Tortoise predation by other corvid species elsewhere appears to be mostly documented in arid areas too. In the Mojave desert, USA, raven predation on Desert Tortoises occurred when ravens expanded into the desert, while in Egypt tortoise predation also occurred in an arid area (Boarman 1992 and Perala 2006) no other records of corvids predating on tortoises have been reported outside arid areas. My analysis on the environmental variables impacting tortoise predation suggests that temperature and rainfall were the factors that most consistently predicted tortoise predation, but these variables were very weak in their overall effect. Perhaps variables that capture water availability in greater resolution (e.g. distance to water sources) would be more effective because it is possible that in areas were water is limited Pied Crows prefer prey with a higher content of water like tortoises rather than seeds. More research is needed to understand which environmental variables can predict tortoise predation and tortoise predation rate.

An alternative explanation for the lack of variables explaining predation probability or rates and the spatial clumping of tortoise predation by crows is that predation may be due to cultural transmission of this behaviour in Pied Crow populations. Culture, in animal behaviour, means an all group behaviour pattern shared by members of animal communities, which are to some degree reliant on socially learned and transmitted information (Laland et al. 2006). Crows have a brain much larger than would be predicted for their body sizes and they display similar intelligent behaviour to the great apes (Emery & Clyaton 2004). Holzhaider et al. (2010) suggest that crows' social system may promote the social transmission of local tool designs, specially favouring the vertical transmission of tool information. Tortoise predation might be one such behaviour learnt by certain parts of the population and transmitted to their offspring. However, crow predation of small Angulate Tortoises was found in the West Coast area during the study, but these tortoise prey remains were found under power-lines and not under any Pied Crow nests monitored in the area. This suggests that the tortoises were depredated by non-breeding Pied Crows, and therefore the behaviour already exists in this population. However, it appears that even if this population of crows has the knowledge of depredating tortoises, this food source is not heavily utilised for feeding the chicks, at least not during the 2016 breeding season.

I found that most tortoise prey remains at Pied Crow nests were Angulate Tortoises. The reason that Angulate Tortoises are the dominant tortoise prey is likely related to their higher abundance compared with the other species. However, it could also be that other species of tortoises are better camouflaged, or that their behaviour differs in other ways which make them less likely to be depredated as a result.

In contrast to my earlier predictions, tortoise abundance did not have an effect on tortoises' predation. However, an alternative explanation for variation in tortoise predation is that it more closely links to the availability of alternative prey for the nestlings. Thus, perhaps information about other prey availability may have a greater influence on tortoise predation. For example, reduced food availability in arid areas might explain why Pied Crows exploit different food sources, such as tortoises. In addition, transects were too few to find a good estimate of the tortoise population, previous rain was not controlled and some areas had insufficient sighting data to asses tortoise densities. Finally, I acknowledge that the variability in timing during the season that transects were conducted could have introduced some biases, although these biases are likely to be small because transects were conducted over 4 weeks of the season (November).

Pied Crows nesting in Namaqualand showed the highest predation rates, which was over twice the predation rates of any other site. One explanation for this is the nature of these nest sites. These nests all occurred along a new power-line that is less than three years old. The area is unlikely then to have been previously exploited by crows, and may be a better source of tortoise prey than areas already previously occupied by Pied Crows. Thus, it may be that predation is higher in this area because the population level effect of Pied Crows has not yet occurred and there are still plentiful young tortoises. If that explanation is correct that assumes that Pied Crows are having a large impact of the size structure of the population. This is believed to have occurred in another population of Speckled Padlopers tortoises in the Northern Cape, where the size class has changed dramatically over the last 15 years, with fewer small animals now present (Loehr 2017). The author of that study has speculated that this could be due to predation by Pied Crows.

Tortoise carapaces found below Pied Crow nests are likely an underestimate of true predation rates. I found that about 10% of the carapaces were removed by scavengers within a 2 weeks period. However, there may be some biases in the methods I used to estimate these scavenging rates. Firstly, due to logistical reasons, I estimated disappearance of carapaces under poles without nests, and not below Pied Crow nests. I would expect scavengers to be more regularly visiting active crow nests, due to other sources of prey that might fall from nest sites, which may increase removal of carapaces.Also, it is possible that the Pied Crows remove tortoise prey remains from under their nest, by themselves, as a nest predation avoidance tactic, where Pied Crow nest predators are more abundant. Second, some of the carapaces I used to test removal rates were old and may be of less resource value to scavengers compared to freshly depredated carapaces which would be removed at higher rates. Third, scavenging might differ spatially. Therefore, I would expect removal rates of freshly depredated tortoises to be higher than those I estimated. Overall, I likely underestimated removal rates, and therefore the true predation tortoise rates are likely more than 10% higher than those I estimated. Nevertheless I expect that my values are unlikely to be largely biased underestimates. Also, it is important to recognise that this sample of nests may not be representative of the predation rates of the population, but may be biased towards higher rates of predation, since I selectively visited some sites with known tortoise predation.

In my study, Pied Crows have clearly depredated only on small tortoises sizes. These size classes include the neonates (2.5 to 4.5 cm) (Branch 1984). Fincham & Lamberts (2014) suggested that counts of tortoise prey remains could be underestimated because Pied Crows might swallow up the youngest tortoises. However, neonates' sizes were included in my findings, suggesting that Pied Crows do not swallow them. However, older age classes up to 70 mm were also found. Therefore, Pied Crows depredate older tortoises than yearlings. Based on the growth rate curve from Branch (1984) it appears that crows depredate on Angulate Tortoises up to 3 years old (6 to 7.5 cm). In Angulate Tortoises, the youngsters have the same growth speed for both sexes, and later, females have a slower growth than males after 6 years old (10 to 11 cm) (Branch 1984).

Then, both sexes would have the same probability to be predated by Pied Crows, although it might not be the same for other species. The reason why I found more males than females could be because males wander more than females during this time of the day and year (Keswick et al. 2006). For other smaller species this may be an even bigger problem since an even larger proportion of the population are exposed to this potential predation, as they will take longer to reach the 70 mm size. This may be especially true for the Common Padloper which is the smallest tortoise in the world. Loehr (2017) surveyed a population of Speckled Padlopers in the Northern Cape in 2000-2004 and 2012-2015 and he found a decline of 66% of the population. Considering the small size of this species, it may be that Pied Crows are playing a role in this decline. However, more research is needed to find out better arguments that show the Pied Crows are reducing tortoises populations.

Considering the critical conservation status of the Geometric tortoise, my nests searching also include an area around a Geometric Tortoise reserve. Geometric Tortoises are smaller than Angulate Tortoises and that can put them in a highest risk from Pied Crow predation. However, only three active nests around the area were found; at none of these were depredated tortoise remains found. However, more effort should be focused on the Geometric Tortoises areas to understand if Pied Crow predation is a potential problem for them. Given their range restricted nature a single problem pair of crows could still do considerable damage to their population. As Pied Crows are opportunistic, they might not depredate them for their low numbers but after an increase on the numbers of Geometric Tortoises, Pied Crows may shift the predator behaviour and decrease their carrying capacity.

In addition to the lack of explanatory power of the environmental variables, we also found very little support to suggest predation was simply a function of overall tortoise abundance. Although, we have too few observations of smaller tortoises (only 1 observed within the size range of depredated tortoises) to explore whether it was a function of tortoise abundance of suitable size. Juvenile (smaller, more cryptic and less active behaviour) tortoises are notoriously difficult to find because of their cryptic behaviour (Branch 1984, Boarman 2003), therefore transects may have been unreliable estimates of their presence. But I am unable to determine if smaller tortoises were absent or if they were too difficult to detect. Understanding if small tortoise availability determines tortoise predation by crows should be an important focus of future research. Moreover, it is not known if the reason Pied Crows are not targeting bigger tortoises is because they are too heavy to carry, suggesting that they still could depredate on them out of the breeding season or because the bigger tortoises are too difficult to kill and extract the flesh. More research is needed to understand why Pied Crows are targeting these size classes.

Although my data suggested that predation by Pied Crows is not as widespread as some people had suspected, there remains the possibility that Pied Crows have already depredated the vast majority of small tortoises in areas where I did not find tortoise predation. In addition, my observations are done only during breeding season, and we do not know how many non breeding crows or reproductive individuals out of breeding season are predating on tortoises or even if some tortoises are not being carried to the nest during breeding season. Also, there is the possibility that Pied Crow breeding season mismatches tortoise nest emergence that might be a tortoise depredation peak. This worrying notion is supported by the very recent study by Loehr (2017). This study found an overall 66% decline in the population of Speckled Padloper in his study area in the Northern Cape over the last 15 years; simultaneously he found a reduction in smaller size classes and reduction in recruitment rates which was thought to have driven the decline. This was attributed to predation by Pied Crows, although little evidence was presented on this issue. With the increasing number of Pied Crows (Cunningham et al. 2016), this problem still needs conservation solutions before the problem is irreversible.

If true however, Pied Crow predation would appear to be an important conservation issue. To understand the mechanism it will be vital to establish if such predation is compensatory (not affecting overall survival of the population) or additive (decreasing survival in prey population). To do so, information is needed both on the crows, for example, predation rates and crow densities, together with information on the tortoises, for example tortoise densities, and fecundity and survival in an area (Kristan & Boarman 2003). The best way to determine the effect of Pied Crow predation on tortoise populations is to evaluate data from actual tortoise populations (Boarman 2003).

I suggest that to mitigate predation on tortoises, an adaptive management approach is needed with feedback on successes and failures guiding a process that is constantly evolving. Long-term management would include more research to better understand Pied Crow ecology with regard to tortoise predation and more long-term surveys on tortoises are needed to understand their populations. The fact that 99% of Pied Crow nests were found in artificial places supports that their increase has been facilitated by human infrastructures. Potentially, Pied Crow numbers could be reduced by habitat alterations; management could remove abandoned windmills or make poles unsuitable in areas with no alternative nest places. A further approach may be to reduce roadkills which may facilitate Pied Crow spread as a main food source (Grant et al. 2017). In the short term, one could discourage nesting behaviour by removing nests with eggs in them because it is known that other species of corvids are not likely to re-nest. Another way is to dip Pied Crow eggs into corn oil, which prevents hatching and causes parents to continue incubating rather than renesting that year (Broaman 2003). Lethal actions should only be implemented as a short term solution and only for Pied Crow pairs that are known to prey heavily on tortoises or in areas where tortoise populations are very important for their conservation. In case of doing a reintroduction tortoise program, release the tortoises only after their straight carapace length is above 75 mm. On the other hand, if Pied Crows are targeting any species of tortoises  smaller than 7 cm, then tortoise prey remains under Pied Crow nests could possibly be used to determine which species of tortoise are present in an area. This is useful, as many species are very difficult to find because of size and crypsis.

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*Appendices*

**Appendix 1**. Results from the plausible models with Δ<2 testing for associations between the presence or absence of tortoise prey remains and Mean day temperature (T), Average rainfall (R), CA1, Ca2, CA3, CA4, Mean NDVI (NDVI), nearest distance to primary roads (R1), nearest distance to secondary roads (R2) and nearest distance to tertiary roads (R3) in each nest site within a buffer of A) 500 meters, B) 1000 meters, and C) 2000 meters. Models are ranked from the most to least supported based on Akaike's Information Criterion (AICc) values. K is number of parameters; Δi is the change in AICc relative to the top model, Wi is the AICc weight, and Dev is the Deviance.

A)

| **Model description** | **K** | **$\Delta_i$** | **$W_i$** | **Dev** |
|---|---|---|---|---|
| **T + R** | 3 | 0.00 | 0.012 | 72.5 |
| **T** | 2 | 0.84 | 0.008 | 75.6 |
| **CA2 + T** | 3 | 1.07 | 0.007 | 73.7 |
| **R** | 2 | 1.14 | 0.007 | 75.9 |
| **CA2 + T + R** | 4 | 1.35 | 0.006 | 71.8 |
| **CA3 + T + R** | 4 | 1.40 | 0.006 | 71.8 |
| **R1 + T + R** | 4 | 1.51 | 0.006 | 71.9 |
| **NDVI + T+ R** | 4 | 1.74 | 0.005 | 72.2 |
| **CA2 + T + CA3** | 4 | 1.81 | 0.005 | 72.2 |
| **R3 + T** | 3 | 1.82 | 0.005 | 74.4 |
| **CA1 + T + R** | 4 | 1.85 | 0.005 | 72.3 |
| **Null** | 1 | | | 84.1 |

**B)**

| Model description | K | $\Delta_i$ | $W_i$ | Dev |
|---|---|---|---|---|
| **T + R** | 3 | 0.00 | 0.017 | 72.3 |
| **T** | 2 | 0.99 | 0.010 | 75.6 |
| **R** | 2 | 1.22 | 0.009 | 75.8 |
| **T + NDVI** | 3 | 1.43 | 0.008 | 73.9 |
| **T + R + NDVI** | 4 | 1.57 | 0.008 | 71.8 |
| **T+ R2** | 3 | 1.61 | 0.007 | 71.9 |
| **T + R3** | 3 | 1.94 | 0.006 | 72.2 |
| **Null** | 1 | | | 84.1 |

**C)**

| Model description | K | $\Delta_i$ | $W_i$ | Dev |
|---|---|---|---|---|
| **T + R** | 3 | 0.00 | 0.012 | 72.4 |
| **T** | 2 | 0.99 | 0.008 | 75.6 |
| **CA1 + T + R** | 4 | 1.15 | 0.007 | 71.4 |
| **R** | 2 | 1.22 | 0.007 | 75.8 |
| **CA1 + R** | 3 | 1.53 | 0.006 | 74.0 |
| **T + R + R2** | 4 | 1.61 | 0.006 | 71.9 |
| **CA2 + T + R** | 4 | 1.71 | 0.005 | 72.0 |
| **CA1 + T** | 3 | 1.72 | 0.005 | 74.2 |
| **CA3 + T + R** | 4 | 1.80 | 0.005 | 72.1 |
| **CA1 + CA2 + T + R** | 5 | 1.91 | 0.005 | 70.0 |
| **R3 + T + R** | 4 | 1.94 | 0.005 | 72.2 |
| **CA4 + T** | 3 | 1.95 | 0.005 | 72.2 |
| **NDVI + T + R** | 4 | 1.99 | 0.005 | 72.3 |
| **Null** | 1 | | | 84.1 |

**Appendix 2**. Results from the plausible models with $\Delta<2$ testing for associations between the presence or absence of tortoise prey remains and Mean day temperature (T), Average rainfall (R), and tortoise abundance (A) in each nest site. Models are ranked from the most to least supported based on Akaike's Information Criterion (AICc) values. K is number of parameters; $\Delta_i$ is the change in AICc relative to the top model, $W_i$ is the AICc weight, and Dev is the Deviance.

| Model description | K | $\Delta_i$ | $W_i$ | Dev |
|---|---|---|---|---|
| **T + R** | 3 | 0.00 | 0.236 | 24.7 |
| **Null** | 1 | 13.97 | 0.001 | 43.2 |

**Appendix 3.** Model parameter estimates for each variable averaged across all plausible models from testing for associations between the presence or absence of tortoise prey remains and Mean day temperature (T), Average rainfall (R), CA1, Ca2, CA3, CA4, Mean NDVI (NDVI), nearest distance to primary roads (R1), nearest distance to secondary roads (R2) and nearest distance to tertiary roads (R3) in each nest site within a buffer of A) 500 meters, B) 1000 meters, and C) 2000 meters.

A)

| | | **Confidence limits** | | |
|---|---|---|---|---|
| **Variable** | **Parameter estimate** | **2.5%** | **97.5%** | **Relative importance** |
| **Intersect** | -1.08 | -45.60 | 4.54 | |
| **T** | 1.31 | -3.09 | 2.65 | 0.88 |
| **R** | -8.96 | -2.12 | 3.27 | 0.75 |
| **CA3** | 3.33 | -5.74 | 1.24 | 0.15 |
| **NDVI** | -3.52 | -1.36 | 6.59 | 0.13 |
| **R3** | 2.09 | -7.73 | 1.19 | 0.12 |
| **CA2** | 1.89 | -6.49 | 1.03 | 0.09 |
| **CA1** | -2.57 | -1.88 | 1.88 | 0.07 |

B)

| Variable | Parameter estimate | Confidence limits 2.5% | Confidence limits 97.5% | Relative importance |
|---|---|---|---|---|
| **Intersect** | -1.09 | -3.16 | 9.78 | |
| **T** | 12.45 | -8.03 | 25.70 | 0.79 |
| **R** | -9.10 | -2.16 | 3.35 | 0.74 |
| **NDVI** | -0.72 | -1.93 | 0.48 | 0.30 |
| **R2** | 0.29 | -4.79 | 10.63 | 0.10 |
| **R3** | 0.25 | -8.35 | 13.36 | 0.09 |

C)

| Variable | Parameter estimate | Confidence limits 2.5% | Confidence limits 97.5% | Relative importance |
|---|---|---|---|---|
| **Intersect** | -1.20 | -3.44 | 1.03 | |
| **T** | 12.78 | -0.14 | 27.04 | 0.79 |
| **R** | -9.12 | -23.06 | 4.82 | 0.82 |
| **CA1** | -0.48 | -13.18 | 0.34 | 0.32 |
| **R2** | 0.29 | -0.47 | 10.63 | 0.08 |
| **CA3** | 0.25 | -0.57 | 10.78 | 0.07 |
| **CA2** | -0.40 | -11.19 | 0.29 | 0.07 |
| **R3** | 0.25 | -0.86 | 13.67 | 0.07 |
| **NDVI** | -30.9 | -165.84 | 103.85 | 0.06 |
| **CA4** | 0.38 | -0.80 | 15.73 | 0.04 |

**Appendix 4.** Model parameter estimates for each variable averaged across all plausible models from associations between the presence or absence of tortoise prey remains and mean day temperature (T), Average rainfall (R), and tortoise abundance (A) in each nest site.

| | | **Confidence limits** | | |
|---|---|---|---|---|
| **Variable** | **Parameter estimate** | **2.5%** | **97.5%** | **Relative importance** |
| **Intersect** | -2.26 | -3.63 | -0.89 | |
| **T** | 2.89 | 0.34 | 5.44 | 1 |
| **R** | -1.74 | -3.19 | -0.29 | 1 |

**Appendix 4**. Results from the plausible models with $\Delta<2$ testing for associations between the count of tortoise prey remains and Mean day temperature (T), Average rainfall (R), CA1, CA2, CA3, CA4, Mean NDVI (NDVI), nearest distance to primary roads (R1), nearest distance to secondary roads (R2) and nearest distance to tertiary roads (R3) in each nest site within a buffer of A) 500 meters, B) 1000 meters, and C) 2000 meters. Models are ranked from the most to least supported based on Akaike's Information Criterion (AICc) values. K is number of parameters; $\Delta_i$ is the change in AICc relative to the top model, $W_i$ is the AICc weight, and Dev is the Deviance.

A)

| **Model description** | **K** | **$\Delta_i$** | **$W_i$** | **Dev** |
|---|---|---|---|---|
| **CA1 + T** | 3 | 0.02 | 0.001 | 763.8 |
| **CA1 + T + R + R** | 5 | 0.09 | 0.004 | 761.2 |
| **CA1 + T + R** | 4 | 0.13 | 0.004 | 762.7 |
| **T + R** | 3 | 0.17 | 0.004 | 764.5 |
| **R + T + R1** | 4 | 0.28 | 0.003 | 763.3 |
| **T** | 2 | 0.57 | 0.003 | 766.3 |
| **CA3 + T + R1 + R** | 5 | 0.61 | 0.003 | 760.5 |
| **CA3 + T + R** | 4 | 0.63 | 0.003 | 762.2 |
| **CA1 + T + R + CA3 + R1** | 6 | 1.02 | 0.002 | 760.2 |
| **CA1 + T + R1** | 4 | 1.06 | 0.002 | 759.4 |
| **CA1 + CA3 + T** | 4 | 1.14 | 0.002 | 763.5 |
| **CA1 + CA3 + T + R** | 5 | 1.14 | 0.002 | 762.9 |
| **CA1 + T + R3 + R** | 5 | 1.15 | 0.002 | 761.3 |
| **R** | 2 | 1.18 | 0.002 | 762.3 |
| **T + R3 + R** | 4 | 1.18 | 0.002 | 767.4 |
| **CA2 + T + R** | 4 | 1.23 | 0.002 | 764.2 |
| **CA3 + T** | 3 | 1.24 | 0.002 | 763.4 |
| **CA1 + CA2 + T** | 4 | 1.25 | 0.002 | 764.9 |
| **CA1 + T + R3** | 4 | 1.28 | 0.002 | 763.8 |
| **CA1 + T + R1 +R3 + R** | 4 | 1.33 | 0.002 | 763.7 |
| **CA1 + CA2 + T + R1 + R** | 6 | 1.35 | 0.002 | 761.1 |
| **CA1+ CA2 + T + R** | 5 | 1.39 | 0.002 | 761.2 |
| **T + R1 + R3 + R** | 5 | 1.48 | 0.002 | 762.6 |
| **CA2 + T + R1 + R** | 5 | 1.50 | 0.002 | 763.2 |
| **CA2 + T** | 3 | 1.51 | 0.002 | 762.5 |
| **CA4 + T + R** | 4 | 1.53 | 0.002 | 765.2 |
| **CA1 + CA4 + T** | 4 | 1.55 | 0.002 | 764.1 |
| **CA1 + T + NDVI** | 4 | 1.56 | 0.002 | 763.6 |
| **CA1 + CA4 + T + R** | 5 | 1.59 | 0.001 | 763.3 |
| **CA1 + R** | 3 | 1.59 | 0.001 | 762.3 |
| **CA1 + CA4 + T + R1 + R** | 6 | 1.66 | 0.001 | 766.4 |
| **CA1 + T + NDVI + R1+ R** | 6 | 1.66 | 0.001 | 761.1 |
| **T + R1** | 3 | 1.70 | 0.001 | 760.6 |
| **R1 + R** | 3 | 1.72 | 0.001 | 766.2 |
| **T + R3** | 3 | 1.76 | 0.001 | 766.9 |

| | | | | |
|---|---|---|---|---|
| **CA4 + T + R1 + R** | 5 | 1.77 | 0.001 | 766.1 |
| **CA1 + T + NDVI + R** | 5 | 1.80 | 0.001 | 763.2 |
| **CA3 + T + R3 + R** | 5 | 1.82 | 0.001 | 762.3 |
| **CA1 + T + R1 + R2 + R** | 6 | 1.86 | 0.001 | 762.2 |
| **CA1 + T + R2** | 4 | 1.87 | 0.001 | 761.0 |
| **T + NDVI + R** | 4 | 1.89 | 0.001 | 763.8 |
| **T + R2 + R** | 4 | 1.95 | 0.001 | 764.3 |
| **T + NDVI + R1 + R** | 5 | 1.95 | 0.001 | 764.4 |
| **CA2 + CA3 + T + R** | 5 | 1.96 | 0.001 | 763.0 |
| **CA3 + R** | 3 | 1.96 | 0.001 | 761.4 |
| **CA2 + T + R2 + R** | 5 | 1.96 | 0.001 | 766.3 |
| **CA3 + T + R1 + R3 + R** | 6 | 1.98 | 0.001 | 763.3 |
| **T + R1 + R2 + R** | 5 | 1.99 | 0.001 | 760.5 |
| **Null** | 1 | | | 769.8 |

**B)**

| **Model description** | **K** | **$\Delta_i$** | **$W_i$** | **Dev** |
|---|---|---|---|---|
| **T + CA1** | 3 | 0.00 | 0.004 | 763.8 |
| **T + CA1 + R1 + R** | 5 | 0.09 | 0.004 | 761.2 |
| **CA1 + T + R** | 4 | 0.13 | 0.004 | 762.7 |
| **R + T** | 3 | 0.17 | 0.004 | 764.5 |
| **R1 + T + R** | 4 | 0.28 | 0.003 | 763.3 |
| **T** | 2 | 0.57 | 0.003 | 766.3 |
| **R1 + T + CA3 + R** | 5 | 0.61 | 0.003 | 763.3 |
| **CA3 + T + R** | 4 | 0.63 | 0.003 | 764.5 |
| **CA1 + T + CA3 + R + R1** | 6 | 1.02 | 0.002 | 761.2 |
| **R + T + CA1** | 4 | 1.06 | 0.002 | 763.5 |
| **CA1 + T + CA3** | 4 | 1.14 | 0.002 | 763.8 |
| **CA1 + CA3 + T + R** | 5 | 1.14 | 0.002 | 762.7 |
| **CA1 + T +R3 + R** | 5 | 1.15 | 0.002 | 762.3 |
| **R** | 2 | 1.18 | 0.002 | 767.4 |
| **T + R +R3** | 4 | 1.18 | 0.002 | 764.2 |
| **CA2 + T + R** | 4 | 1.23 | 0.002 | 763.3 |
| **CA3 + T** | 3 | 1.24 | 0.002 | 766.2 |
| **CA1 + CA2 + T** | 4 | 1.25 | 0.002 | 762.7 |
| **CA1 + T+ R3** | 4 | 1.28 | 0.002 | 763.8 |
| **CA1 + T + R1 + R3** | 5 | 1.33 | 0.002 | 763.7 |
| **CA1 + T + CA2 + R1 + R** | 6 | 1.35 | 0.002 | 763.4 |
| **CA1 + T+ CA2 + R** | 5 | 1.39 | 0.002 | 761.2 |
| **T + R1 + R3 + R** | 5 | 1.48 | 0.002 | 762.7 |
| **C2 + T + R1 + R** | 5 | 1.50 | 0.002 | 763.2 |
| **CA2 + T** | 3 | 1.51 | 0.002 | 761.9 |
| **CA4 + T + R** | 4 | 1.53 | 0.002 | 764.4 |
| **CA1 + CA4 + T** | 4 | 1.55 | 0.002 | 764.1 |

| | | | | |
|---|---|---|---|---|
| **CA1 + T + NDVI** | 4 | 1.56 | 0.002 | 763.6 |
| **CA1 + CA4 + T + R** | 5 | 1.59 | 0.001 | 762.8 |
| **CA1 + R** | 1 | 1.59 | 0.001 | 762.3 |
| **CA1 + CA4 + R1 + R** | 5 | 1.66 | 0.001 | 766.4 |
| **CA1 + T + NDVI + R1 + R** | 6 | 1.66 | 0.001 | 765.8 |
| **T + R1** | 3 | 1.70 | 0.001 | 760.6 |
| **R1 + R** | 3 | 1.72 | 0.001 | 766.2 |
| **T + R3** | 3 | 1.76 | 0.001 | 766.9 |
| **C4 + T + R1 + R** | 5 | 1.77 | 0.001 | 766.1 |
| **CA1 + T + NDVI + R** | 5 | 1.80 | 0.001 | 763.2 |
| **CA3 + T + R3 + R** | 5 | 1.82 | 0.001 | 762.4 |
| **CA1 + T + R1 + R2 + R** | 6 | 1.86 | 0.001 | 764.2 |
| **CA1 + T + R2** | 2 | 1.87 | 0.001 | 761.0 |
| **T + NDVI + R** | 2 | 1.89 | 0.001 | 763.8 |
| **T + R2 + R** | 2 | 1.95 | 0.001 | 764.1 |
| **T + NDVI + R1 + R** | 5 | 1.95 | 0.001 | 764.4 |
| **CA2 + CA3 + T + R** | 5 | 1.96 | 0.001 | 762.6 |
| **CA3 + R** | 3 | 1.96 | 0.001 | 763.3 |
| **CA1 + T + R2 + R** | 5 | 1.96 | 0.001 | 767.4 |
| **CA3 + T + R1 + R3 + R** | 6 | 1.98 | 0.001 | 762.6 |
| **T + R1 + R2 + R** | 5 | 1.99 | 0.001 | 763.2 |
| **Null** | 1 | | | 763.1 |

**C)**

| **Model description** | **K** | **$\Delta_i$** | **$W_i$** | **Dev** |
|---|---|---|---|---|
| **CA1 + CA3 + R1 + R + T** | 6 | 0 | 0.003 | 758.5 |
| **CA1 + T** | 3 | 0.98 | 0.003 | 763.6 |
| **CA1 + T +R1 + R** | 5 | 1.00 | 0.003 | 761.2 |
| **CA1 + CA3 + T + R1** | 5 | 1.02 | 0.003 | 760.0 |
| **CA1 + CA3 + T** | 4 | 1.11 | 0.002 | 761.5 |
| **CA1 + T + R1** | 4 | 1.34 | 0.002 | 762.6 |
| **T + R** | 3 | 1.38 | 0.002 | 764.5 |
| **CA1 + T + R** | 4 | 1.42 | 0.002 | 763.1 |
| **T + R1 + R** | 4 | 1.49 | 0.002 | 763.3 |
| **CA1 + CA3 + T + NDVI + R1** | 6 | 1.51 | 0.002 | 759.1 |
| **CA3 + T + R1 + R** | 5 | 1.53 | 0.002 | 761.1 |
| **CA1 + CA3 + NDVI + R1 + R + T** | 7 | 1.56 | 0.002 | 758.1 |
| **CA1 + CA3 + T + R** | 5 | 1.66 | 0.002 | 758.5 |
| **CA3 + T + R** | 4 | 1.73 | 0.002 | 758.1 |
| **T** | 2 | 1.77 | 0.002 | 761.1 |
| **CA1 + CA3 + T + R1 + R3 + R** | 5 | 1.78 | 0.002 | 762.7 |
| **CA3 + T + NDVI + R1 + R3 + R** | 5 | 1.83 | 0.002 | 766.3 |
| **CA1 + T + NDVI + R1 + R3 + R** | 5 | 1.91 | 0.001 | 758.1 |
| **CA1 + T + NDVI** | 4 | 1.97 | 0.001 | 759.6 |

| | | | | |
|---|---|---|---|---|
| **CA1 + T + NDVI + R1** | 5 | 1.97 | 0.001 | 763.2 |
| **CA3 + T** | 3 | 1.97 | 0.001 | 761.9 |
| **CA1 + T + R3** | 4 | 1.99 | 0.001 | 764. |
| **Null** | 1 | | | 763.2 |

**Appendix 5**. Results from the plausible models with $\Delta<2$ testing for associations between the count of tortoise prey remains and Mean day temperature (T), Average rainfall (R), and tortoise abundance (A) in each nest site. Models are ranked from the most to least supported based on Akaike's Information Criterion (AICc) values. K is number of parameters; $\Delta_i$ is the change in AICc relative to the top model, $W_i$ is the AICc weight, and Dev is the Deviance.

| **Model description** | **K** | **$\Delta_i$** | **$W_i$** | **Dev** |
|---|---|---|---|---|
| **T + R** | 3 | 0 | 0.176 | 267.1 |
| **T + R + A** | 4 | 0.38 | 0.145 | 267.2 |
| **Null** | 1 | 7.60 | 0.003 | 273.2 |

**Appendix 6.** Model parameter estimates for each variable averaged across all plausible models from associations between the count of tortoise prey remains and mean day temperature (T), Average rainfall (R), CA1, CA2, CA3, CA4, Mean NDVI (NDVI), nearest distance to primary roads (R1), nearest distance to secondary roads (R2) and nearest distance to tertiary roads (R3) in each nest site within a buffer of A) 500 meters, B) 1000 meters, and C) 2000 meters.

A)

| | | Confidence limits | | |
|---|---|---|---|---|
| **Variable** | **Parameter estimate** | **2.5%** | **97.5%** | **Relative importance** |
| **Intersect** | 0.73 | -1.03783 | 2.502362 | |
| **CA1** | 0.75 | -0.43 | 1.93 | 0.49 |
| **T** | 1.18 | -0.05 | 2.43 | 0.93 |
| **R1** | -0.67 | -2.04 | 0.70 | 0.37 |
| **R** | -1.02 | -2.60 | 0.54 | 0.72 |
| **CA3** | 0.54 | -0.48 | 1.56 | 0.22 |
| **R3** | -0.34 | -1.47 | 0.78 | 0.16 |
| **CA2** | 0.23 | -0.98 | 1.45 | 0.14 |
| **CA4** | -0.15 | -1.26 | 0.95 | 0.09 |
| **NDVI** | -0.22 | -1.19 | 0.74 | 0.08 |
| **R2** | -0.17 | -1.10 | 0.74 | 0.06 |

B)

| Variable | Parameter estimate | Confidence limits |  | Relative importance |
|---|---|---|---|---|
|  |  | 2.5% | 97.5% |  |
| **Intersect** | 0.71 | -1.10 | 2.53 |  |
| **T** | 1.16 | -0.08 | 2.41 | 0.93 |
| **CA1** | 0.75 | -0.61 | 2.11 | 0.53 |
| **R** | -0.93 | -2.56 | 0.68 | 0.70 |
| **R1** | -0.66 | -2.04 | 0.71 | 0.34 |
| **CA2** | 0.37 | -1.55 | 2.30 | 0.20 |
| **NDVI** | -0.49 | -1.93 | 0.94 | 0.13 |
| **R3** | -0.35 | -1.48 | 0.77 | 0.12 |
| **CA4** | -0.15 | -1.27 | 0.95 | 0.07 |
| **CA3** | -0.09 | -1.04 | 0.85 | 0.12 |
| **R2** | -0.17 | -1.09 | 0.75 | 0.07 |

**C)**

| Variable | Parameter estimate | Confidence limits<br>2.5% | <br>97.5% | Relative importance |
|---|---|---|---|---|
| **Intersect** | 0.71 | -0.93 | 2.36 | |
| **T** | 1.46 | 0.13 | 2.79 | 1.00 |
| **R** | -0.84 | -2.53 | 0.84 | 0.57 |
| **CA1** | -0.95 | -2.29 | 0.39 | 0.74 |
| **CA3** | -0.67 | -1.59 | 0.25 | 0.57 |
| **R1** | -0.88 | -2.25 | 0.49 | 0.58 |
| **NDVI** | -0.48 | -1.79 | 0.83 | 0.21 |
| **R3** | -0.41 | -1.54 | 0.71 | 0.09 |

**Appendix 7.** Model parameter estimates for each variable averaged across all plausible models from associations between the count of tortoise prey remains and mean day temperature (T), Average rainfall (R), and tortoise abundance (A) in each nest site.

| Variable | Parameter estimate | Confidence limits<br>2.5% | <br>97.5% | Relative importance |
|---|---|---|---|---|
| **Intersect** | 3.17 | 0.71 | 5.63 | |
| **T** | 2.58 | -0.33 | 5.51 | 0.82 |
| **R** | -2.56 | -5.38 | 0.25 | 0.83 |
| **A** | 0.16 | -2.58 | 2.91 | 0.46 |