



Foraging efficiencies and species'
distributions: An explanation of the range
expansion of the Hadedda Ibis (*Bostrychia*
***hagedash*) in relation to soil moisture.**

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I dedicate this work to my grandfather, Frederick Duckworth, 1929-2008.

Abstract

The influence of soil moisture on the foraging time needed to meet BMR (foraging efficiency) in *hadedas* was explored in Cape Town, South Africa. This was done by monitoring *hadedas* foraging and recording the successful prey items eaten per minute on soils of different moisture. BMR was calculated using a published method and diet calorimetry was used to determine the amount of energy in their diet. Results indicate that *hadedas* are able to forage most efficiently at intermediate soil moistures ($0.40 - 0.80 \text{ cm}^3 \cdot \text{cm}^{-3}$) whilst at either low or high soil moisture they are less efficient. The optimum soil moisture was $0.68 \text{ cm}^3 \cdot \text{cm}^{-3}$, which enabled *hadedas* to forage for only 1.81 hours per day to meet BMR, in contrast to $0.17 \text{ cm}^3 \cdot \text{cm}^{-3}$, at which *hadedas* must forage for 4.1 hours. These results suggest that soil moisture may have influenced the range expansion of *hadedas* in the last 50 years.

Introduction

Species distributions are postulated to be limited by two main processes; abiotic and biotic factors (Molles 2005, Root 1988). Abiotic factors, such as climate, can limit species' distributions for example if a species cannot tolerate frost or if the prevailing weather often prevents the species from foraging (Molles 2005). Individual organisms have evolved characteristics that enable them to survive a suite of environments, however, no single species may tolerate the full range of earth's environments (Molles 2005). Biotic factors refer to ^{amongst others} intra and interspecific interactions such as competition and predation that may limit the distribution of species (Root 1988). There is some debate in the literature as to which of these factors is more influential in determining species' distribution ranges. Andrewartha & Birch (1954) suggested, with support from Caughley (1984), Root (1988), ^{and} Molles (2005), that abiotic factors may be the more dominant ecological process, although this has been contested (MacArthur 1958).

Nonetheless, neither abiotic nor biotic factors act independently on individuals, and observed species' distribution are often a result of pressure exerted by both factors

simultaneously. Therefore it is important to recognise the combined influence of factors that limit species' distribution ranges in order to understand their current distributions, and to accurately predict future movements and expansions. Such limiting factors are difficult to measure, however, and often many limiting factors will go unmeasured. Due to the influence of multiple unmeasured factors the causal relationship between one measured variable and ecological processes may be vague. Traditional regression techniques using the mean of response and predictive variables may reveal a weak relationship, or even none (Cade and Noon 2003). This makes naming one factor that may ultimately limit species' distributions problematic. In cases like these it is more useful to analyse the boundaries of response variables rather than the mean (Cade and Noon 2003). Such analyses are termed Quantile Regression, which estimates rates of change from the minimum to the maximum response of a response variable. In effect, this allows for a more complete view as to what effect a predictor variable is having on different levels of the response variable (Cade and Noon 2003). One such field that has extensively found use for such an analyses is optimal foraging strategy.

Optimal foraging strategy models take into account multiple limiting biotic and abiotic factors, and aim to describe how organisms should partition their time and activities (i.e. energy expenditure) in order to gain maximum food energy in minimal time (Bautista *et al.*, 1998, Nolet 2001, Jodice *et al.*, 2002). Foraging has two basic components: time spent searching for food, and time spent handling food. In high food density environments feeding efficiency (the number of food items obtained per unit time; Nolet 2001) is limited almost entirely by the time spent handling food by the foraging species, as searching for food does not present a limitation, and essentially they are feeding at their maximum efficiency (Molles 2005). However, in food limited environments, searching for food presents a limitation. In response, organisms may alter their behavioural (Bautista *et al.*, 1998, Nolet 2001, Molles 2005) or anatomical characteristics (Dykstra and Karasov 1992). Consequentially, their feeding efficiency is relatively low.

Climate is one factor among many that influences food availability (Molles 2005) as it influences food production, water supply, habitat, and foraging conditions (Caughley 1987, Molles 2005). Climate is therefore one limiting factor to feeding efficiency.

Food availability is of profound importance, because it directly influences foraging time. If foraging time can be kept to a minimum, more time can be spent on other activities such as attending and feeding offspring, avoiding predators, mating and social interactions. Individuals should adjust their activity budgets in a way that maximises fitness and optimal foraging is therefore a key strategy for the success of an organism (Fryxell and Lundberg 1997, Bautista *et al.*, 1998, Nolet 2001, Molles 2005). A species should occur in regions where the climate allows a high enough feeding efficiency for its individuals to survive and reproduce. If organisms do not occur in these regions, it suggests that other factors such as competition, predation or abiotic factors not directly associated with feeding are limiting them from doing so (Westoby 1984).

One such method in which we may gauge the feeding efficiency of individuals is through their basal metabolic rate (BMR). The basal metabolic rate (BMR) is the minimum metabolic rate of inactive, post absorptive endotherms whilst in their rest phase in a thermal neutral zone (Williams and Tieleman 2000, McNab 2003, McKechnie 2007). Essentially this is the amount of energy needed to sustain life, and anything below this threshold results in death (Sherwood *et al.*, 2005). Although individuals in nature rarely ever function at their BMR, this variable is useful in comparing energetic expenditures across taxa (Williams and Tieleman 2000, McKechnie 2007). Any type of activity, such as locomotion, foraging or escaping predators will require more energy than that needed to meet the BMR.

In birds, extensive studies have examined BMR and optimal foraging strategies in order to explain population distributions and expansions (Williams and Tieleman 2000, Root 1988, Jodice *et al.*, 2002, Bautista *et al.*, 1998). These studies have shown that BMR and feeding efficiency of birds affects their distributions considerably. This study aims to use this method to explain the distribution patterns of the hadeda ibis (*Bostrychia hagedash*, hereafter called the hadeda). The distribution of the hadeda has increased since at least 1910, and dramatically so since the 1950s (MacDonald *et al.*, 1986). Originally populations were confined to the eastern, and south eastern parts of Southern Africa, with the southwestern limit being Knysna. In the 1950s major range expansions into the southwestern Cape, the Karoo, the grasslands of the eastern Cape, Transvaal highveld and the free state were observed. Smaller expansions in a western

direction along the Zambezi, Okavango, Limpopo and Orange river also occurred (Harrison *et al.*, 1997). The species' range in South Africa increased from 530 900 km² in 1910 to 1 323 300 km² in 1985 (MacDonald *et al.*, 1986). Westward Range expansions have continued since 1985, and sightings of Hadedas were recorded as far as Alexander bay and the Orange River mouth in 1995 (Harrison *et al.*, 1997).

Reasons for the range expansions up until 1985 have been proposed by MacDonald *et al.* (1986). They hypothesised that hadedas have adapted to human habitation, and that an indirect effect of human activities is the expansion of hadeda population ranges. For example, an increase in the plantation of trees (mostly alien, MacDonald *et al.*, 1986) in formerly treeless areas provides nesting and perching habitats. Also, an increase in the irrigation of previously arid regions provides perennial feeding grounds. Since hadedas originally occurred in the wetter eastern parts of South Africa, rainfall may also affect its distribution. These reasons may still account for the continued range expansion observed today. This study explores one possible mechanism limiting the hadeda's range, by analysing the feeding efficiency of hadedas in relation to soil moisture. Soft, moist soil is critical for feeding in this species that extracts earth worms and other invertebrates from the ground (MacDonald *et al.*, 1986, Hockey *et al.*, 2005). Essentially, I aim to find out for how long hadedas need to forage on different substrates to meet their BMR. I hypothesise that hadedas will feed more efficiently on very moist soils, such that soil moisture and feeding efficiency are strongly positively correlated. Therefore, I predict that hadedas will be able to forage at near optimal levels on soils with high moisture contents. I hope that this knowledge help in accurately predicting future population movements and expansions, both in relation climate change and human land use change.

Methods and Materials

Focal Species

Hadedas Ibises are large wading birds (adults; 76cm, 1.32kg) that belong to the family Plataleidae. In natural settings, they usually inhabit moist grasslands, savannas, marshes, flooded grasslands and occur along well vegetated river courses. However, as a result of human habitat alteration, they are additionally found on lawns and in gardens, suburban areas and agricultural lands (Harrison *et al.*, 1997, Hockey *et al.* 2005).

Hadedas are sedentary, but can be nomadic in response to localized rainfall events. They usually forage in pairs or small family groups (Hockey *et al.*, 2005). Flock sizes constitute anywhere between 5-40 individuals depending on the area (Hockey *et al.*, 2005). They are apparently monogamous long-term breeders, and often nest in trees which overhang or are in close proximity to water bodies. However, they have been found to nest far distances from water bodies as a result of habitat alteration (Harrison *et al.*, 1997). They lay 1 to 4 eggs and fledge up to 3 young per breeding attempt. The same pair can raise several broods per year. In the Cape Town area, the main breeding season is between June and November, but a few breeding pairs can be found at any time of the year (Hockey *et al.*, 2005). No good survival estimates exist to date.

Do they
breed in
summer in
these
rainfall
areas?
bleddy + time

The hadedas' diet consist mainly of earthworms and other invertebrates that they extract from soft ground, however they have been known to eat small vertebrates (such as lizards, fish and reptiles; Hockey *et al.*, 2005). They are able to forage in wetlands or in soft soil and mud and feed mainly by touch, rather than sight.

Hadedas forage for food that is just below the soil surface by inserting their beaks into the soil. When they have caught a food item, they withdraw their beaks from the soil with the food item in their beak, and they have a characteristic 'head bob' during which they swallow the food item. This characteristic 'head bob' gave me a reliable signal as to whether or not a food item was eaten. Where the situation allowed, I tried

to distinguish between an earthworm and other invertebrates. Three classes of food type were recorded; earthworm, other invertebrate and not sure. *No vertebrates!*

Study sites and general procedure

This study was conducted on various fields in Cape Town, in the ^{Province} Western Cape of South Africa. Field work was completed between May 14 and 22 September 2008. I only considered the feeding efficiency of hadedas foraging on terrestrial grounds. Open grass patches, parks, gardens, schools, the banks of as well as estuaries, sports grounds and fields were searched for hadedas. Once hadedas were sighted, their feeding efficiency was recorded and then soil moisture readings were taken.

Feeding efficiency

The number of successful food items eaten by a hadeda in a selected period of time was recorded. Initially I started out observing hadedas foraging for 5 minutes, but reduced this to 3 and then to 1 minute to be able to define the foraging area more precisely (the birds move slowly around whilst they probe the soil for food). For the analysis, I use the number of prey captured per minute of foraging. To ensure a high degree of accuracy, binoculars and terrestrial scopes were used and only one hadeda was observed per time unit. Extreme caution was taken to ensure that the same individual was not observed twice. Additionally, sites where hadedas were observed where varied as much as possible to avoid re-observing an individual.

Soil moisture content

Soil moisture content was measured with a Moisture Meter Device (type HH2, version 2), product of Delta-T devices Ltd 2002. The Moisture Meter Device consisted of a hand held Moisture Meter attached by a RS232 cable with 9-way to 25-way converter to a thetaprobe. To obtain soil moisture readings, the thetaprobe was thrust into the soil at study sites, and readings were displayed digitally through the hand held Moisture Meter. The readings are expressed as volume of water present in a cubic meter of soil.

During fieldwork, soil moisture readings were taken from the soil upon which hadedas foraged for the observation time. In most cases, hadedas foraged broadly, and therefore special care was taken to ensure that moisture readings were taken from the area of soil upon which they foraged for majority of the observation time. If the foraging individual covered a heterogeneous area, a number of readings were taken and the average of these values was then used for the analysis.

Diet calorimetry

To be able to quantify the amount of foraging time required to meet their BMR, the energy content in hadedas' prey was measured. Earthworms constitute a large portion of the diet of hadedas (Hockey *et al.*, 2005), and for this reason, I decided to calculate the energy contained within a single earthworm. Earthworms of the species *Aporrectodea caliginosa* were collected from a compost heap in Cape Town, because they have been frequently observed as hadeda prey (Pers. Obs.). Five of these were analysed for their energy contents. Earthworms were dried in a drying oven at 70°C for 72 hours, weighed (to the nearest milligram) and crushed into powder form for analysis in the bomb calorimeter.

Basal Metabolic Rate

I calculated the BMR for hadedas from the allometric relationship between body weight and BMR. I used three published allometric relationships and verified that the results were broadly consistent. These relationships were:

- | | |
|---|------------------|
| (1) $\text{Log (BMR)} = 0.699 * \text{log (Mb)} - 1.371$ | McKechnie (2006) |
| (2) $\text{Log (BMR)} = \text{log (3.19)} + 0.73 * \text{log (Mb)}$ | Root (1988) |
| (3) $\text{BMR} = (3.19) \text{ Mb}^{0.75}$ | Repasky(1991) |

where;

log (BMR) is expressed in Watts (eqn. 1) or kj/d (eqn. 2), and

log Mb is the log of the average weight of an adult hadeda in grams.

For comparison, I converted all measures of BMR into kj/d.

Statistical Analyses

Since I view soil moisture as one of many potential factors limiting the feeding efficiency of hadedas, I used quantile regression on the 90th percentile (Cade and Noon 2003). I expected soil moisture to affect the maximum number of prey hadedas can obtain per minute, and the 90th percentile was the highest percentile that permitted a satisfactory model fit. The results were qualitatively the same if I used the 85th or 80th percentiles. All analyses were carried out in programme R, v. 2.7.2, with add-on package 'quantreg' (R Development Core Team 2008).

Results

Hadedas feeding ecology

A total of 73 hadedas were observed foraging, and all feeds were independent of each other (as far as could be controlled). Recall that for the analysis, the number of successful feeds per minute was used. The range of prey items caught per minute was between 0 (soil moisture $0.348 \text{ cm}^3 \cdot \text{cm}^{-3}$) and 10 ($0.780 \text{ cm}^3 \cdot \text{cm}^{-3}$). This included earthworms and unidentified prey items. Moisture values ranged between $0.167 \text{ cm}^3 \cdot \text{cm}^{-3}$ to complete saturation (i.e. $1.00 \text{ cm}^3 \cdot \text{cm}^{-3}$). For a given moisture value, there was a large amount of ^{Overlap}variation within feeds/minute. For example, at a moisture of $0.42 \text{ cm}^3 \cdot \text{cm}^{-3}$ hadedas caught one to nine prey items per minute, and at a moisture $0.70 \text{ cm}^3 \cdot \text{cm}^{-3}$ caught between two and seven prey items (Figure 1).

I expected soil moisture to limit the maximum number of prey items hadedas can obtain from the soil, and I used a quantile regression on the 90th percentile to examine this hypothesis. The analysis revealed that the maximum number of prey caught per minute increased with soil moisture up to a certain point, and then decreased again. The best fitting regression line was: number of feeds = $0.87 + 25.08 \times \text{moisture} - 18.58 \times \text{moisture}^2$ (Figure 1). Both moisture terms were significant ($p=0.006$, $t=4.682$ and $p=0.032$, $t=-3.638$ respectively). Significance for moisture was also achieved at the 80th and 85th percentile.

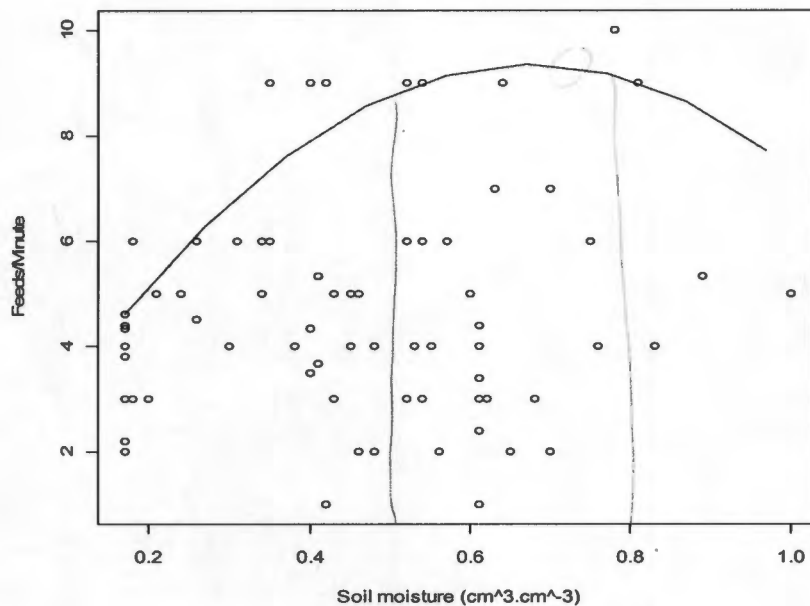
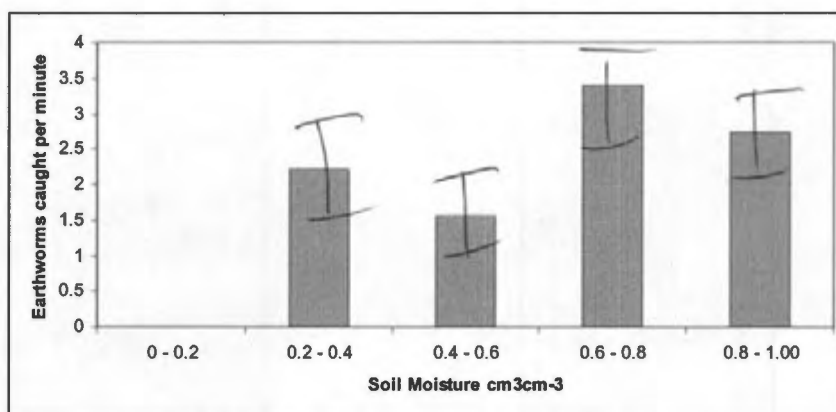


Figure 1. Number of prey items caught by hadedas feeding on lawns that differed in soil in moisture. The line is the best fitting quantile regression line for 90th percentiles.

Figure one shows that feeds per minute were the least at high and low values for soil moisture. The highest feeds per minute were obtained for soil moisture values between 0.5 and 0.8 $\text{cm}^3.\text{cm}^{-3}$. The highest feeds/minute are predicted to be at 9.33, at a soil moisture of 0.68 $\text{cm}^3.\text{cm}^{-3}$ based on the fitted line from figure 1.

52% of all hadedas observed consumed earthworms, and at least 29% of hadedas' diet was composed of earthworms. Although ^{the} number of earthworms caught per minute was not significantly correlated with soil moisture, more earthworms were caught at high soil moistures (Figure 2).



Significant difference?

Figure 2. The number of earthworms caught per minute as per different ranges of soil moisture (cm³.cm⁻³).

Diet calorimetry and BMR calculations

Bomb calorimetric analysis on the earthworm species *Aporrectodea caliginosa* returned an average value of 19.45 kJ/g (dry weight). The average dry weight of a single earthworm, based on a sample of 30 earthworms, was 0.27 grams. Therefore, each worm contained on average 5.20 kJ of energy.

Standard deviation?

BMR was calculated using an average weight of 1.32 kg (n=64, Hockey *et al.*, 2005). There was a high level of agreement between the three methods of calculating BMR based on allometric relationships. The method based on McKechnie (2006) returned a value of 23.26 kJ/h, whilst the other two (Root 1988, and Klieber 1930) both returned a value of 25.21 kJ/h. For the analysis, we utilised the former because it is based on an allometric relationship fitted to non-passerine birds (to which *hadedas* belong).

Number of feeding hours required to meet BMR

Converting

My observations and the results of the calorimetric analysis allowed me to calculate a rough estimate of how much energy *hadedas* maximally took in per time unit. This was done by multiplying the predicted feeds/minute values from the model in figure 1 by the energy content of an earthworm (i.e. 5.2 kJ) and converting to kJ/d. I am justified in using energy content of an earthworm as a proxy for the energy content of all prey because at the very least (using a conservative observation method), 29% of

hadedas' diet consists of earthworms, and because there is little variation in energy content across invertebrate families (Salonen *et al.*, 1976; Wacasey and Atkinson 1987). However, this is assuming that hadedas can convert 100% of an earthworm's energy, which is clearly an overestimate. Roughly, only 10% of energy is transferred from one trophic level to the next (Campbell *et al.*, 2002). Owing to this, the amount of energy taken in per day by hadedas was divided by 10 to give a more realistic estimate. Then, the calculated BMR of hadedas (in kJ/d) was divided by the amount of energy gained per day in order to calculate the number of feeding hours required to meet BMR per day. The results are depicted in figure 3.

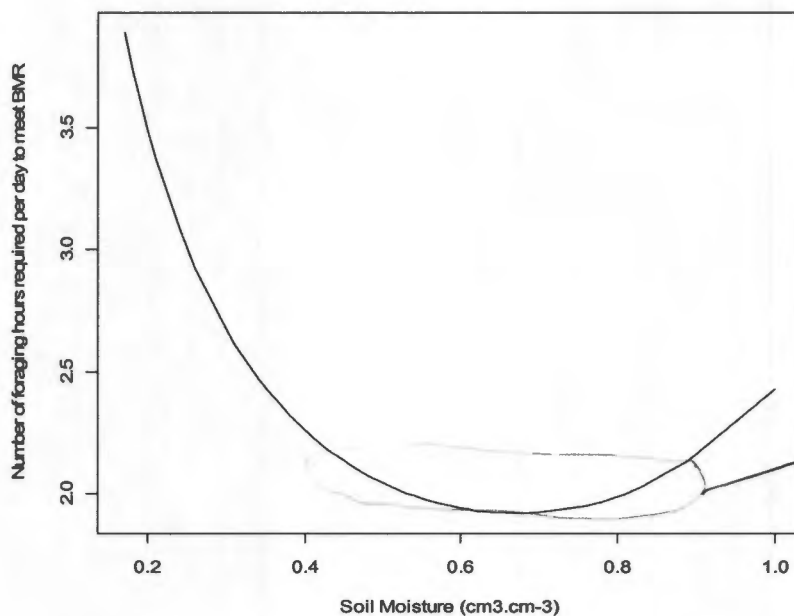


Figure 3. Number of foraging hours required per day to meet BMR for hadedas. This line is based on the fitted values from figure 1.

Figure three illustrates that there is a considerable difference in the time taken to meet BMR depending on which soils hadedas forage upon, as expected. Moderate values of soil moisture, between 0.5 and 0.8 cm³.cm⁻³, provide optimal foraging grounds, whilst on either very dry or moist soils hadedas must forage for longer. For example, 1.81 hours was the least amount of foraging time required to meet BMR, which occurs at a soil moisture value of 0.68 cm³.cm⁻³. In contrast, a hadeda foraging on soil of moisture 0.17 cm³.cm⁻³, would take 3.89 hours to meet BMR, over twice as long. At full saturation, they would have to forage 1.33 times as long.

(1988) that suggest there exists a degree of influence by abiotic factors on the range of species, and in this case, *hadedas*.

Organisms rarely, if ever, function at their BMR (McKechnie 2007; Williams 2000). This measurement is primarily used to compare energy expenditures across taxa (McNab 2003). Any form of physical activity will require additional energy over that of the BMR. For example, Goldstein (1988) estimated that long flights for birds averaged out to 11 times BMR. Short flights for birds are much higher. Tatner & Bryant (1986) estimated that a short intense flight cost european robins 23 times their BMR. *Hadedas* probably spend most of their time walking rather than flying, but the energy requirements for this activity are less well known and depend on walking speed, weight and size of the bird (Goldstein 1988). Owing to the fact that not all birds are geometrically similar, there is no general figure for the energetic cost of walking or running. The cost of foraging also is difficult to measure. However, the Gambel's quail (*Callipepla gambelii*) walks and forages simultaneously (as does the *hadedas*), and foraging costs were estimated at 3.5 times BMR (Tatner 1986). If the foraging cost for *hadedas* can be assumed to be close to this, the influence on foraging time needed to make up for this activity is extensive. For example, on soils of moistures of $0.7 \text{ cm}^3.\text{cm}^{-3}$ instead of foraging for 1.81 hours to meet BMR, *hadedas* must forage for 6.33 hours to make up the costs of this activity. Comparatively, at saturation ($1.00 \text{ cm}^3.\text{cm}^{-3}$), they would need to forage for 8.49 hours as opposed to 2.42. On soils of $0.17 \text{ cm}^3.\text{cm}^{-3}$, instead of foraging for 3.72 hours to meet BMR, they must forage for 13.03 hours. Since this figure represents foraging time needed to meet foraging costs only, and it seems unlikely that *hadedas* forage for more than 12 hours a day, one can hypothesise that they cannot occur in areas where soil moisture regularly drops below this level. At this point, these comparative values are merely speculative as the foraging costs of *hadedas* are unknown. What is of interest is the influence soil moisture has on foraging time. Therefore, depending on how many times higher daily energy expenditure (DEE) is than BMR, it may be vital that *hadedas* forage on soils of optimal moisture.

The influence of unmeasured factors on feeding efficiency must not be overlooked. This study focussed on soil moisture, viewed as one of the chief factors limiting maximum feeding efficiency of *hadedas* (Hockey *et al.*, 2005, MacDonald *et al.*,

Discussion

I examined the feeding rate of hadedas in relation to soil moisture, and my results suggest that hadedas are able to forage more efficiently at moderate values for soil moisture. Soil moisture is probably one factor limiting the hadedas' ability to feed and may influence where this species can persist. My results are consistent with the notion that irrigated lawns have been an important factor enabling the hadedas to expand its range (MacDonald *et al.*, 1986).

The relationship between feeding efficiency and foraging minutes required to meet BMR and soil moisture was not linear, as hypothesised, but rather quadratic (Figure 1). Soil invertebrate densities are expected to correlate with soil moisture conditions up to a value of around $0.40 - 0.85 \text{ cm}^3 \cdot \text{cm}^{-3}$, depending on the soil type (El-Duweini and Ghabbour 1965, Staly *et al.*, 2007). Thereafter they decrease in density with increasing soil moisture. This relationship mirrors the results found in this study regarding feeding efficiency, as feeding efficiency is obviously a function of invertebrate density. It was found that feeding efficiency on the 90th percentile was optimum at a range of soil moisture values between 0.40 and $0.80 \text{ cm}^3 \cdot \text{cm}^{-3}$, and outside of this range foraging efficiency decreased substantially (Figure 1). Despite this, earthworms caught per minute was the highest at high moisture values (Figure 2). Earthworms conform to the same distribution trend of invertebrates with regard to rainfall (El-Duweini and Ghabbour 1965; Zaller and Arnone 1999). However, at high soil moisture levels they are forced to the soil surface because they are starved of oxygen as water enters their burrows. Once at the soil surface, they are killed rapidly by ultra-violet light (Lee 1951). Thus, although they do not occur in higher densities at higher moisture levels, they are easier to prey upon, which accounts for why more earthworms were at high moisture values.

Not
exactly
 $0.8 - 1.0$
lower
than
 $0.6 - 0.8$

The foraging time taken to meet hadedas' BMR depends significantly on the soil moisture (Figure 3). 1.81 hours was the shortest foraging time predicted to meet BMR, at $0.68 \text{ cm}^3 \cdot \text{cm}^{-3}$ moisture. At $0.1 \text{ cm}^3 \cdot \text{cm}^{-3}$ moisture hadedas would need to forage for 4.3 hours to meet BMR, over 2.31 times longer, and at full saturation ($100 \text{ cm}^3 \cdot \text{cm}^{-3}$) around 1.33 times longer. Taken together, these results support numerous other studies, for example Andrewartha and Birch (1954), Caughley (1984), and Root

1986). Of course it is not the only limiting factor. Other limiting factors such as prey availability, predation, flock size and composition (Matthysen 1999), interspecific competition (Dann and Norman 2006) or even unidentified unmeasured factors could influence the foraging success (Cade and Noon 2003). It is expected that multiple unmeasured limiting factors affected feeding efficiency in this study considering I looked at only one limiting factor among many. Multiple unmeasured factors increase the heterogeneity of organism's response (Cade and Noon 2003) and may account for large variations in datasets. For example, 3 feeds/minute were obtained at a soil moisture range between 0.17 and 0.68 $\text{cm}^3.\text{cm}^{-3}$, and 4 feeds/minute were obtained at a moisture range between 0.17 and 0.83 $\text{cm}^3.\text{cm}^{-3}$. Additionally, due to high natural variation in soil moisture (Zaller and Arnone 1999), there may have been some uncertainty in soil moisture measurements in observations where hadedas foraged over a heterogeneous area. Quantile regression analysis was used to account for the influence of these unmeasured factors (Cade and Noon 2003). No standard deviation / error

The result in figure 3 is associated with a degree of uncertainty in the measurements for the energy of earthworms. For this calculation, one species of earthworm from one locality in Cape Town was considered for calorimetric analysis; after which the amount of energy taken in by hadedas per day was calculated. Not all prey items were earthworms, and earthworms eaten were not all of the same species, and of the same size. Therefore, this too, may give an unrealistic estimate of the energy gained by a hadeda in one minute. If the average value of energy calculated is actually more than the real value, the amount of energy gained per minute would be an overestimate, and therefore an underestimate of the number of feeding hours required to meet BMR. If the amount of energy calculated is actually less than the real value, then the opposite is true. In light of this, I view my estimate in figure 3 to be an underestimate of the actual time needed to forage to meet BMR. This is because mostly large adult worms were used for the calorimetric analysis, which therefore biases the result and overestimates the amount of energy gained per minute. Nonetheless, this result still provides a quantitative description of the least amount of time hadedas may forage for per soil moisture. I have provided an analysis into one mechanism that limits hadedas range distribution and expansion, and considers it from a single perspective among many. Nonetheless, this analysis using coarse data has found a significant relationship between soil moisture and feeding efficiency. Future studies should aim to quantify as

accurately as possible the amount of energy hadedas obtain in a time period, as difficult as this may seem, as well as accounting for other potential limiting factors. I believe that the results would be quantitatively the same as in this study.

The range expansion of hadedas over the last 50 years has been due to land-use changes that convert previously arid regions into moist grasslands via artificial watering (MacDonald *et al.*, 1986), as well as increased plantation of alien trees. This study confirms that hadedas are able to feed more efficiently on moderately moist soils, and are therefore able to forage for less time to meet their BMR than on arid or semi-saturated soils. Despite only investigating one aspect of the range expansion through feeding efficiency, and one aspect of feeding efficiency through soil moisture, I am able to state that lawns of the right moisture offer a habitat where hadedas may feed efficiently. From this I conclude that soil of the right moisture values may have been an important factor in hadeda range expansions. Lawns of optimal moisture have a strong link to climate; either it rains often enough such that soils of optimal moisture occur more often, or because people have enough water to irrigate large areas. The next step in the overall understanding of hadeda range expansion is to quantify exact energy gains per time, as well as DEE, and relate this to soil moisture to analyse if there is a significant critical relationship.

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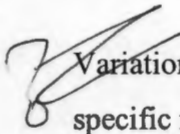
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