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Molokwu, Mary

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Mary Ngozi Molokwu

Department of Biology
Animal Ecology
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LUNDS UNIVERSITET

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Mary Ngozi Molokwu

AKADEMISK AVHANDLING
Som för avläggande av filosofie doktorsexamen vid naturvetenskapliga fakulteten, Lunds Universitet kommer att offentligen försvaras i Blå Hallen, Ekologihuset, Sölvegatan 37, Lund, fredagen den 29 Oktober 2010, Klockan 10.00.

ACADEMIC DISSERTATION
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Dr Christopher J Whelan
Department of Biological Sciences
University of Illinois, Chicago

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Dissertation
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Abstract

This study evaluates the costs associated with foraging for birds in a savannah woodland area in central Nigeria. Specifically, it looks at the following questions: 1) how does seasonal variability in food and water availability affect the value of resources to birds in dry environments? 2) Does proximity to water affect foraging decisions? What implication will this have in the management of savannah birds? 3) Are tropical birds mostly affected by metabolic or predation costs? 4) What factors affect diet selection in birds and how? 5) How are birds adapted to hot dry environments? I carried out experiments in the field and in an aviary and provided artificial food patches, consisting of feeding trays with seeds mixed in sand or pebbles (in the aviary study). I used the giving-up density (GUD; amount of food left in a depletable patch after a foraging bout) of birds as a behavioral indicator and compared GUDs between different microhabitats, varying in levels of predation risk or thermal hazard, across different seasons and between years. In one study, I also placed out water pots to observe the effects of water on foraging, in another I looked at the diet selection strategy of birds offered two seed types differing in energetic content and in another looked at the effect of temperature on birds. Results showed that temporal (seasonal) variations in GUDs appear to be driven by food availability and water while small-scale spatial variation in GUDs seems to be driven by predation risk. Although birds seem to be willing to trade-off food for thermoregulation, they may resort to more costly means of thermoregulation e.g. hyperthermia (elevation of body temperature), when energy demand increases. Also proximity to drinking water will affect the extent to which granivorous birds exploit their environment and the diet selection strategy employed by these birds may be largely dependent on seed quality. My studies have revealed that the behavior observed among animals is shaped by the circumstances they are faced with in their environment. Therefore foraging behavior can be used to evaluate the magnitude and significance of the effects of the different costs associated with a foraging area and may serve as a useful tool in conservation.

Key words: foraging behavior, seasonality, predation risk, granivorous birds, food availability, water, temperature, savannah, dry tropics, energy, secondary compounds, diet selection

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To my parents,
Aya Joseph and Elizabeth Molokwu
for being a pillar of support

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II Olsson O. and Molokwu M.N. (2007) On the missed opportunity cost, GUD and estimating environmental quality. Isreal Journal of Ecology and Evolution 53:263-278. 47

III Molokwu M.N., Nilsson J-Å., Ottosson U., and Olsson O (2010) Effects of season, water and predation risk on patch use by birds of an African savannah. Oecologia. doi: 10.1007/s00442-010-1781-3. 65

IV Molokwu M.N., Nilsson J-Å., and Olsson O. Diet selection in birds: trade-off between energetic content and other qualities of seeds. Submitted. 81

V Nilsson J-Å., Molokwu M.N. and Olsson O. The use of hyperthermia in hot environments. Manuscript. 99

VI Molokwu M.N., Nilsson J-Å., Onoja J.D. and Olsson O. Effects of temperature on food intake in savannah birds. Manuscript. 107

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Costs of foraging in a dry tropical environment

PRELUDE

On a sunny morning in a semi-arid area in Africa, a small granivorous bird is ready to begin its daily activity, the most important of which is to find food in order to gain energy required to avoid starvation and be in good condition at reproduction. It moves around on the bare ground and finds a small patch of broken pieces of dry grass straws that form a layer over the soil. Tossing aside the litter with its bill, it searches for fallen grass seeds buried in the sand. Patches will vary in quality and quantity; which patches will be worth spending time in? What foods will be more valuable to handle or process? This bird has to act fast, lest it becomes food itself for a bird of prey. Even in the absence of predation danger, as midday approaches the cost of remaining in the scorching sun increases. It is also the dry season and a long distance to the nearest waterhole. What choices will be optimal? What decisions will make the best balance of food and safety?

In this thesis, I evaluate the costs associated with foraging for birds in a savannah woodland area in central Nigeria. I investigate the relationship between seasonality in food and water availability, predation risk and thermal stress and examine the role each factor plays in shaping the foraging behavior of birds in this dry, seasonal environment.

INTRODUCTION

Foraging ecology and behavior

One very important resource that determines how well an animal performs in its environment is the local density and immediate availability of food (Begon et al. 1996; Leisler 1992). Animals require food to obtain energy necessary to maintain body processes and for growth and reproduction (Schmidt-Nielsen 1997). Hence the process of obtaining food is directly linked to fitness. When an animal forages for food, it is faced with a number of options which include where to feed, what to eat or whether to continue feeding or not (MacArthur and Pianka 1966; Emlen 1966; Stephens et al. 1986), as well as how long to remain in a foraging patch (Charnov 1976; Stehens et al. 1986). A forager may be constrained by its internal state, its physiology or morphology and by different external factors, biotic or abiotic (Stephens and Krebs 1986; Houston et al. 1993; Sih and Christensen 2001; Stephens et al. 2007). These constraining factors set limits to the extent to which an animal can exploit its environment and therefore affects its foraging decisions.

Foraging animals are continuously faced with different forms of challenges and risks. The extent to which they are affected by potential danger depends to a great extent on habitat structure. For example the structure of a habitat may influence a forager's decision by creating different habitat sub-units differing in food availability and quality, predation risk and thermal stress. While moving between these microhabitats, they will have to avoid being casualties to imminent danger while at the same time avoiding the likelihood of starving to death (Stephens et al. 2007). The more time it spends foraging, the higher the energy reward, but also the greater the risks of falling victim to danger. This results in a trade-off of some sort (Lima 1985). Hence foraging decisions can have direct consequences on energy intake and survival and will thereby affect fitness (Olsson et al. 2002).

Two models have formed the basis for other models of foraging theory: the diet and patch models. While the diet model deals with the decision whether to attack an encountered food item or not, the patch model deals mainly with how animals should allocate time to patch exploitation (Stephens and Krebs 1986; Stephens et al. 2007). These first models have however undergone significant modifications over the years (Stephens et al. 2007). For example, the original model that describes how an animal should use a patch, the marginal value theorem (MVT) states that a foraging animal should leave a patch when its marginal rate of intake equals the average rate of intake for the entire environment (Charnov 1976), assuming that the forager is working towards maximizing its energy intake rate. However, an important consideration may be the extent to which animals will maximize net intake rates of energy when they are continuously faced with different conflicting selective pressures such as competition, predation, thermal stress, water balance and nutrient requirements (Walsberg 1983). In addition, animals in the wild are not constantly foraging, but engage in other fitness-related activities such as mating, territoriality, nest building as well as feather maintenance (Brown 1988). As a response to this, an extension of the MVT (Brown 1988) incorporates a complete set of costs that may influence the forager's patch leaving decisions. The model states that a forager should quit foraging when the benefits derived from being in a patch no longer outweigh the costs. The model assumes that the resources in the forager's environment are depletable and that it can engage in other fitness related activities aside from foraging (Brown 1988).

The amount of food left in a depletable patch after a foraging bout, i.e. giving-up density (GUD; Brown 1988) reflects the quitting harvest rate at the point where a forager leaves the patch. This is affected by the costs of foraging in that patch (Kotler and Brown 1990). This is expressed by

$$H = C + P + MOC \qquad \text{(Equation 1)}$$

where H is the quitting harvest rate, C, metabolic costs, P, predation costs (how much energetic compensation a forager will demand for taking a risk) and MOC, missed opportunity costs (costs of forgone alternatives such as foraging elsewhere or engaging in other fitness related activities). When the benefit of feeding in a patch no longer outweighs the costs incurred by the forager, i.e. when the quitting harvest rate is equal to the sum of the metabolic, predation and missed opportunity costs of foraging, the best option is to leave that patch (Brown 1988). GUD is used as a surrogate of the quitting harvest rate and should increase with any increase in the metabolic, predation and missed opportunity costs (Brown 1988, 1992).

Early diet models addressed issues related to attack and handling of food before consumption and the inclusion of food items are based on their profitabilities (Pulliam 1974). Later models combined elements of the diet selection and patch use theory to model within patch diet selection when exploiting patches with multiple resources (Brown and Mitchell 1989; Brown and Morgan 1995). More recent models have gone a step further to incorporate processes that take place after food is consumed (post-consumptive handling; Whelan and Schmidt 2007). These models combine the physiological and ecological aspects influencing diet choice and patch use. The acquisition and handling of food will be influenced by the physiological processes that follow consumption (Whelan and Brown 2005; Whelan and Schmidt 2007). Consequently, a forager's physiological capacity will determine the variation in its diet.

Foraging behavior gives insight into the experiences of organisms in their environment, which in turn shapes the evolution and coadaptation of other traits such as its physiology and morphology (Ydenberg et al. 2007). The evolutionary consequences of feeding behaviors and the resulting population and community

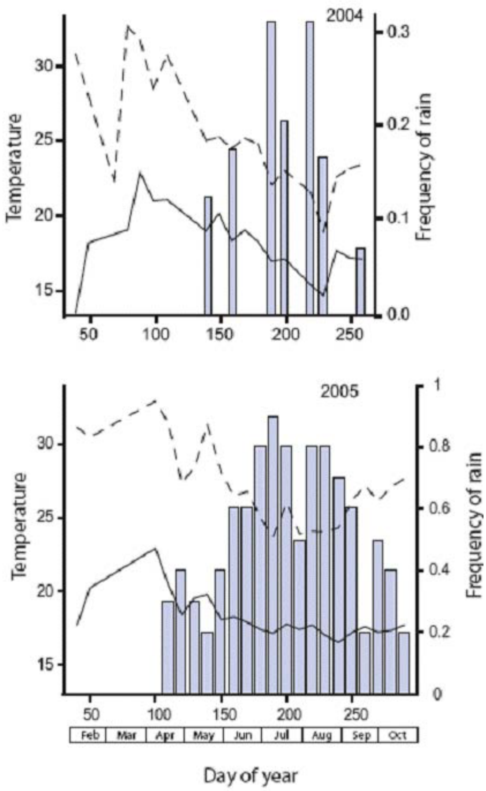

Figure 1. Maximum and minimum temperatures (solid and dashed lines, respectively) and frequency of rain (bars) during February to October in (a) 2004 and (b) 2005. Day 1 refers to 6 and 8 February respectively.

structure form the basis of foraging ecology (Ydenberg et al. 2007).

The significance of foraging behavior

Foraging models assume that the feeding behavior of animals are shaped by natural selection and that the individuals that exhibit behaviors that tend to increase fitness will contribute more genes to future generations. Such traits will be heritable and through natural selection will eventually become dominant in populations of that species (Emlen 1966; Werner and Hall 1974; Pyke 1984; Stephens and Krebs 1986). This notion was supported by the use of mathematical models (optimization models; Stephens and Krebs 1986) to investigate the set of decisions in the foraging process that will produce the best outcomes. This gave rise to the concept of "optimal foraging theory" (Stephens and Krebs 1986; Stephens et al. 2007).

If animals are designed to act optimally, then studying their behavior may provide ecologists with information on their assessment of the environment. For example, food abundance can be measured directly by sampling food availability in the environment (Hutto 1990; Crowley and Garnett 1999; Olsson et al. 2001). However, estimating food availability in an environment based on direct sampling may not accurately reflect its availability to an animal (Hutto 1990; Olsson et al. 1999; 2001; Persson and Stenberg 2006). Observation of a forager's behavior in its environment may therefore result in better estimations of environmental quality as well as the effects of biological interactions such as predation and competition. An individual will assess opportunities and hazards in its environment and respond through its behavior (Brown 2000). Foraging behavior could therefore serve as a useful tool in conservation (Rosenzweig 2007) such as in monitoring population changes (Whelan and Jedlicka 2007).

Dry environments

Tropical savannahs are characterized by low rainfall and high temperatures with large seasonal and annual variation (Nix 1983) and consequential strong seasonal changes in vegetation structure and productivity (Hopkins 1968), which are determined mainly by rainfall patterns (Fig. 1). Hence animals adapted to these regions are constantly faced with fluctuations in food and water availability (Walker 1985). These environments are made up of two main seasons, the dry and wet seasons. In addition to temporal variation in vegetation condition and production there is also great spatial variation (Bourliere and Hadley 1970) resulting from burning and grazing pressures as well as other anthropogenic activities. This may result in a landscape mosaic of habitats that vary in structure and function, e.g. protective cover, food and water availability. Such temporal and spatial variability in food availability and habitat structure is of utmost importance to consumers (Bourliere and Hadley 1970) and coupled with temporal and spatial changes in the thermal environment will form a significant component of the foraging ecology of granivores (Bozinovic and Vasquez 1999; Caraco et al. 1990).

Optimal foraging models have mainly been tested on temperate birds (e.g. Olsson and Holmgren 1999; Olsson et al. 1999; 2001; 2002; Oyugi and Brown 2003; van Gils et al. 2005; Nolet et al. 2006). However, the ecological models should be valid in both temperate and tropical climates, although environmental conditions are so different that the outcomes may differ substantially.

In this thesis, I explore the different costs that may be faced by foraging birds in a dry, seasonal environment. My research questions are the following:

1. How does seasonal variability in food and water availability affect the value of resources to birds in dry environments? (Paper I, II & III)
2. Does proximity to water affect foraging decisions? What implication will this have in the management of savannah birds? (Paper III & IV)
3. Are tropical birds mostly affected by metabolic or predation costs? (Paper III)
4. What factors affect diet selection in birds and how? (Paper IV)
5. How are birds adapted to hot dry environments? (Paper III, V, VI)

METHOD

Study Area

The entire study was carried out at the field station of the A. P. Leventis Ornithological Research Institute (Fig. 2), located within the Amurum Forest Reserve 15 km east of Jos, Central Nigeria 09°53′N 08°59′E (Fig. 3). The Reserve, with a total area of about 125 ha, comprises a small area of granitic outcrops in dry scrub savanna, interspersed with gallery forests, patches of grassland (Fig. 4) and surrounded by cultivated farmlands on the Jos Plateau (Ezealor 2002). Some common tree species include *Daniella oliveri, Parkia biglobosa, Acacia albida, Lophira lanceolata, Khaya senegalensis, Vitex doniana, Piliostigma thonningii* and *Ficus spp* (Ezealor 2002). Rain occurs from around May to August, while the dry season is between October and March with an average rainfall of ca. 1400 mm per year (Payne 1998). Temperature range is between +20 - +25 °C (< +10 °C in extreme cases) during the coldest months and +30 - +35 °C during warm and dry months (Paper I).

Field studies

Giving-up density: In my field studies (Paper I, III and IV), I have used artificial food patches in the natural environment, consisting of feeding trays with seeds mixed in sand (Fig. 5). In all cases I have allowed free-ranging birds to forage from the trays. I placed out seed trays (Fig. 6) in the morning around 7 am and collected and weighed the remaining seeds (GUDs) after about five hours.

Focal observations: I carried out focal observations to record the identity of the foragers. I observed the feeding patches from about 10 m away, with the use of a telescope (Paper I and III) and recorded the species that visited the tables by speaking into a tape recorder. I observed a focal individual to collect data on vigilance and feeding rates. However the data on vigilance behavior is not presented in this thesis.

In Paper I and III, several granivorous bird

Figure 2. Left photo: Aerial view of the A. P. Leventis Ornithological Research Institute (APLORI) field station. Right photo: Institute building. Photo by Ola Olsson.

Figure 3. Map of Nigeria. Arrow points to the study area in Jos, central Nigeria. Inset: map of Africa with arrow pointing to Nigeria.

Figure 4. Photo shows the different habitat types within the Amurum Forest Reserve. Left photo: fringing forest, top right: savanna area, bottom right: a view of the Reserve from the top of an inselberg, showing rocky out crops, an area of savanna woodland and a strip of fringing forest. Photo by Ola Olsson.

Figure 5. The author placing seed trays and a water pot at a feeding station. Photo by Ola Olsson.

Figure 6. Top: a feeding tray with mixture of sand and millet. Bottom: Grey headed sparrows feeding from a tray (Photo by Martin Stervander).

Figure 7. Top left – right: red-cheeked cordon bleu, cinnamon breasted rock bunting, lavender waxbill, rock firefinch. Bottom left – right: speckle-fronted weaver, village weaver, bronze manikin, red-billed firefinch. Photos taken from the APLORI website (www.aplori.org) bird gallery.

species visited the artificial patches, however at different frequencies. These are sun lark *Galerida modesta*, village weaver *Ploceus cucullatus*, red-billed fire-finch *Lagonosticta senegala,* cinnamon-breasted rock bunting *Emberiza tahapisi.* speckle-fronted weaver *Sporopipes frontalis*, northern red bishop *Euplectes franciscanus*, rock firefinch *Lagonosticta sanguinodorsalis,* lavender waxbill *Estrilda caerulescens,* orange-cheeked waxbill *Estrilda melpoda* and red-cheeked cordon-bleu *Uraeginthus bengalus* (Fig. 7). In both studies, the same sites were used and the food in a feeding tray consisted of pearl millet Pennisetum gambiense seeds mixed in sand. I looked at the effect of a seasonal change in food (Paper I and III) and water availability (Paper III) by collecting a continuous series of GUD data throughout the year, covering different seasons, thus, looking for a seasonal trend in GUDs (Paper I). I also placed feeding patches in the open and in a bush microhabitat in Paper I while in Paper III, I placed patches in the open, close to bush and near bush to separate the effects of predation risk and heat (Fig. 8). At the same time, I looked at the seasonal variation in microhabitat use in both studies.

The study in Paper IV took place in a separate site and only one bird species, village weaver, was observed to visit the patches. I investigated how the quality and abundance of different food types determined the diet selection strategy of these birds by presenting wild birds with two food patches placed side by side, at different distances from a bush. Each feeding tray contained different proportions of millet and peanut *Arachis hypogaea* seeds (Fig. 9) mixed together in sand. The two seed types were used because of their differences in chemical composition, especially in energy content. In another experiment in the same study, I placed two feeding trays, containing only millet or only peanuts, side by side (Fig. 9), at different distances from cover and at different seasons, to investigate how diet selection varied

Figure 8. Feeding tables placed in a bush, near bush and in the open.

Figure 9. Left: Mixture of millet and crushed peanuts; top: crushed peanut seeds; bottom: millet seeds.

with season.

In paper V, we mist-netted birds during two periods of the day early in the morning and late afternoon and measured body temperature within five minutes of capture. We used a copper thermocouple to measure body temperature by inserting it into the cloaca (Fig. 10; see Paper V for more detail). Ambient temperature was also recorded at the same time. This was to investigate the change in body temperature with ambient temperature, to understand the physiological adaptations of birds living in dry, hot environments.

Aviary studies

I also carried out experiments in an aviary (Paper VI; Fig. 11) consisting of three compartments: one with ambient temperature, another heated to temperatures well above ambient temperature, with a fan heater and a third cooled to low temperatures by an air conditioner. I recorded the food intake, i.e. amount of seeds eaten, of two bird species, red-cheeked cordon-bleu and northern red bishop, in these different compartments, by allowing them to choose between feeding in each compartment. This was to investigate the extent to which birds are affected by temperature (metabolic costs) and to understand the different adaptations of these birds to their environment.

Figure 10. Prof. Jan-Åke Nilsson taking body temperature of a bird with a copper thermocouple, while the author takes readings. Photo by Jacinta Abalaka.

FORAGING COSTS

In a seasonal environment such as in the dry tropics, variation in food and water availability and temperature, as well as the timing of seasonal activities should influence the costs of foraging in various ways (Fig. 12). In his patch-use model, Brown (1988) states that a forager should leave a patch when its quitting harvest rate equals the sum of its metabolic, predation and missed opportunity costs. Equation 1 can be rewritten as:

$$\mathrm{H} = c + \frac{\mu F}{\partial F/\partial e} + \frac{\Phi}{p(\partial F/\partial e)} \text{.......... Equation (2)}$$

Where $\mathrm{P} = \frac{\mu F}{\partial F/\partial e}$, and $\mathrm{MOC} = \frac{\Phi}{p(\partial F/\partial e)}$

Cost of predation and Missed opportunity cost

Figure 11. Aviary with three compartments.

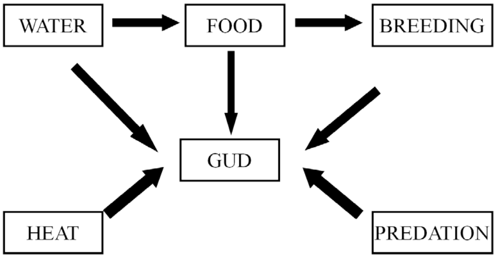

Figure 12. Schematic representation of the different factors that potentially can affect GUD.

The cost of predation (P), which is the energetic compensation a forager will demand for taking a risk (Brown 1992; Brown and Kotler 2004) is made up of three components: the risk of predation (μ), survivor's fitness i.e. the expected fitness if surviving (F) and the marginal value of energy i.e. the rate of change in expected fitness with energy intake (∂F/∂e). A change in any of these components of the cost of predation will affect GUD. P should increase with an increase in μ and F, and increase with a decrease in ∂F/∂e. Within its environment a foraging animal is faced with microhabitats that differ in risk and while seeking for food it risks the possibility of becoming food for other animals. Consequently, it has to set a balance between food and safety (Lima 1985), spending more time and feeding more in safer habitats even if the energy reward in the risky habitat is greater (Brown and Kotler 2004). The forager accepts a lower rate of energy gain rather than maximizing its energy intake rate. It should therefore demand much more to feed in the risky habitat, resulting in a higher cost of predation (see review by Brown and Kotler 2004; Paper II). A rich body of literature has shown that animals perceive greater risk with increasing distance from cover (see Brown and Kotler 2004 for a review). Hence bushes may serve as refuge from predation.

Animals living in different environments face different circumstances and so will have different fitness prospects (Olsson et al. 2002). This may influence the manner in which they respond to risks and will be reflected in their cost of predation. The cost of predation is not the same as the risk of predation, instead, it is the price (measured in energy units) placed on the consequences of a risky venture (Brown and Kotler 2004). Therefore, an individual in a high quality environment (high F) will demand more for taking a risk, i.e. will have a higher cost of predation than an individual with a lower fitness expectation (low F) and thus should be less willing to take risks (Olsson et al. 2002). However, in making between environment comparisons, the missed opportunity cost is the most vital cost of interest (Paper II).

The missed opportunity cost (MOC) is the cost of forgoing other alternative activities, including foraging elsewhere, while foraging in a patch (Brown 1988; Paper II). It consists of three components: the long-term survival rate, p; the marginal value of energy, ∂F/∂e and the marginal value of time, Φ (i.e. the change in expected fitness if given one extra time unit). Therefore, MOC should be affected by an increase in other activities such as territorial defense, mating, nest building, as well as by resource availability (Paper II). It should increase with an increase in Φ, a decrease in p and a decrease in ∂F/∂e. While many studies have assumed that the cost of predation is the most important cost that determines the behavior of animal in (e.g. Olsson et al. 2002; Brown 1992; Brown and Kotler 2004), we argue that when making within environment comparisons, that is not the whole truth (Paper II). Instead, between environment differences in food availability will influence the MOC. Since the opportunity to feed in other patches in the environment is part of the opportunity cost, the

Figure 13. Photo showing the same savannah area during dry and wet seasons.

higher the quality of the environment (e.g. higher food availability), the more the lost opportunities i.e. higher MOC.
An increase in food availability in the environment increases the value of other alternative activities, increasing the MOC, through both an increase in the marginal value of time and a decrease in the marginal value of energy (eq. 2; Paper I, II, III). This is because while in the current patch, the forager continuously misses the opportunity to forage in other rich patches. In the same vein MOC may differ between seasons, either due to a difference in resource availability or a difference in the frequency of certain activities such as between breeding and non-breeding seasons (Paper I & III).

In our study on the seasonal variation in foraging behavior of birds in a seasonal environment (Paper I), GUD of foraging birds seemed to follow the pattern of grass seed availability between dry and wet seasons (Fig. 13). In the beginning of the dry season, when seed availability is still moderately available (Dostine et al. 2001), GUDs were still high, however as food availability decreased, towards the beginning of the wet season, GUDs declined and reached its lowest point at the beginning of the rains when seed availability was most likely at its lowest level (Fig. 14, Paper I). When food became more available, either due to an increase in insect abundance (Denlinger 1980) or when grass seeds became more available after the rains (Crowley and Garnett 1999; Dostine et al. 2001), GUDs increased further (Paper I & III). The increase in GUD when food availability increased was possibly due to a decrease in the marginal value of food, which resulted in an increase in the MOC and P. In contrast, when food availability is low, the marginal value of food should increase, resulting in a low MOC and P. Thus, MOC and possibly P should differ between rich and poor seasons.

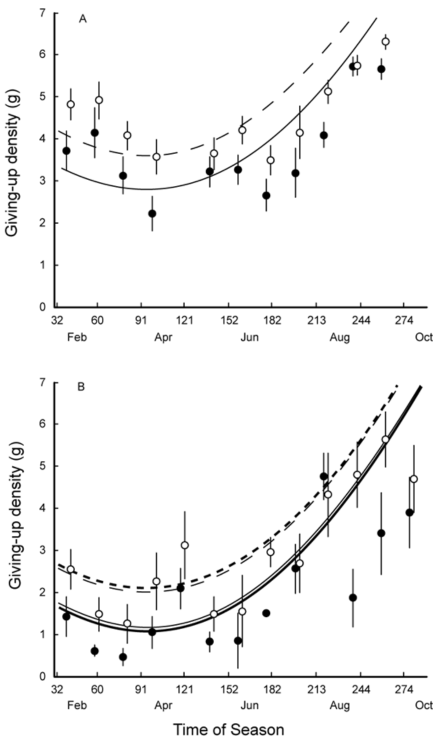

Figure 14. Mean (± SE) GUD, in g of remaining millet seeds, during February to October in two microhabitats, cover (shaded circles) and open (open circles), over the season in (a) 2004 and (b) 2005. Curves represent patterns predicted by models 19 (bold line) and 22 (thin line). In 2004, both models yeild identical results but in 2005 GUD in open (dashed lines) and cover (solid lines) differs slightly between the two models. Each symbol represents a 20-day average.

Similarly, in the study on the effects of seasonality, water and predation risk on birds (Paper III), a difference in GUD between seasons may result from a difference in MOC as well as in P. However, in addition to the seasonal variation in GUD, there was a difference in GUD, within seasons between patches with or without water. During seasons with high food availability but low water availability, providing water increased GUDs, meaning that birds fed less thoroughly when water was provided. This is most likely due to an increase in MOC, resulting from increasing opportunities of feeding elsewhere. Proximity to water should increase the value of food and in a rich environment (or season), this results in

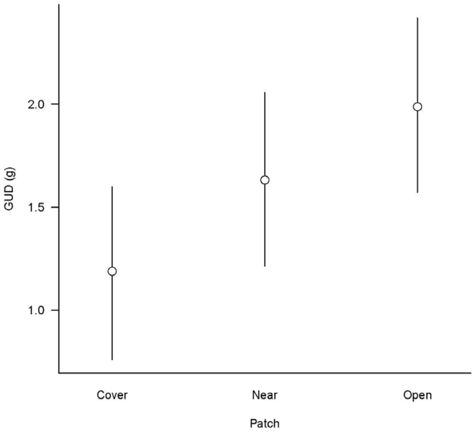

Figure 15. Giving-up densities, measured as the mass of seeds (g) remaining in the food patch after a foraging session, on food patches placed in a bush (cover), close to a bush (near; <2 m from a bush) and in the open (~8 m from the closest bush). Error bars represent 95 % confidence intervals, and the values shown are representative for absence of water during the dry season.

a further increase in environmental and patch quality, thereby resulting in less depletion of patches. Thus the MOC should increase even if the cost of predation P remains the same. A similar result was obtained in Paper IV. In contrast, during the season with low food and water availability, GUD decreased when water was provided i.e. birds fed more thoroughly when water was provided. Since the environment was relatively poor at this time, providing water may have only increased the value of the foraging patch, leading to a more thorough depletion of the patch. This may have led to a decrease in the MOC and possibly P. The effect of water provision that leads to low GUDs have been explored to a great extent in other studies (Kotler et al. 1998; Hochman and Kotler 2006; Shrader et al. 2008), however, this is the first demonstration of an increase in GUD with water provision.

In Paper I, I placed feeding patches in open and bush microhabitats, possibly differing in predation risk and thermal costs. Open microhabitats may be viewed as costly in terms of predation risk, i.e. if being in the open increases the chances of being seen and attacked by a predator, or in terms of thermal stress, if exposure to high temperatures increases metabolic costs. Birds fed more in cover during the two years of the study (Fig. 14), possibly due to a higher cost of predation or high metabolic cost in the open. Preference for cover remained unchanged throughout the year, irrespective of variations in food availability and temperature across seasons. A higher cost of predation may outweigh any metabolic costs as has been suggested in previous studies (Brown et al 1994), which I tested in Paper III.

In the study on the effects of seasonality, water and predation risk on patch use (Paper III), I placed patches in bush, close to a bush and far away from a bush, to separate the costs of predation and thermal stress. There was a gradient in patch use, as birds had the lowest GUDs in bush and the highest GUDs in the open. The patches close to a bush had intermediate values (Fig. 15). This and the fact that the pattern remained the same across seasons points to predation risk as the main factor affecting microhabitat use in these birds and suggests that predation costs are higher than metabolic costs for birds in this environment. This is not surprising as birds have physiological adaptations by which they can offset metabolic costs (Paper V).

Metabolic cost

The metabolic cost is the energetic costs associated with foraging. An important part of this cost is usually the thermal costs associated with the foraging area, i.e. the thermal environment. Animals have successfully adapted to a range of ambient temperatures. The range of thermal environments that minimize metabolic rate is called the thermoneutral zone (McNab 2002) and this is delimited by the upper and lower critical temperature, respectively. Above, as well as below this range of ambient temperatures animals have to thermoregulate (McNab 2002).

Behavioral thermoregulation may include selection of less thermally stressful microhabitats, reduction in activity during the daily peak in temperature (Tieleman and Williams 2002) or adoption of different positions or body postures to regulate temperature.

Animals expend energy while searching for and consuming food and in a hot and dry environment, the energetic costs should increase with a decrease in food and water supply (Louw 1993). Then foraging animals will have to search longer, exposing themselves to harsh weather conditions and increasing metabolic costs. Foraging animals have been found to reduce activity during periods of high temperatures (Kenagy et al. 2004) and higher GUDs in the open have sometimes been attributed to high metabolic costs (Bozinovic and Vasquez 1999; Kilpatrick 2003). However, in a study on hoopoe larks (Alaemon alaudipes; Tieleman and Williams 2002) birds spent less time feeding and more time resting during the hotter part of the day, only on days with surplus food. On days without supplemented food, they increased their exposure to heat and spent more time feeding (Tieleman and Williams 2002). Therefore a trade-off may exist between foraging and thermoregulation.

Most studies that suggest a behavioral avoidance of thermally costly microhabitats, e.g. seeking shade or spending less time feeding under heat stress, have been carried out on rodents (e.g. degus Octodon degus; Bozinovic and Vasquez 1999; Bozinovic et al 2000; Bacigalupe et al. 2003; Kenagy et al. 2004). Most of these animals lack the physiological adaptations to cope with heat stress, for example, degus lacks the capacity for evaporative cooling (Bacigalupe et al. 2003). Birds on the other hand, in addition to behavioral adaptations, possess physiological mechanism with which they can offset metabolic costs. In attempting to tease apart metabolic and predation costs, all arguments point to predation

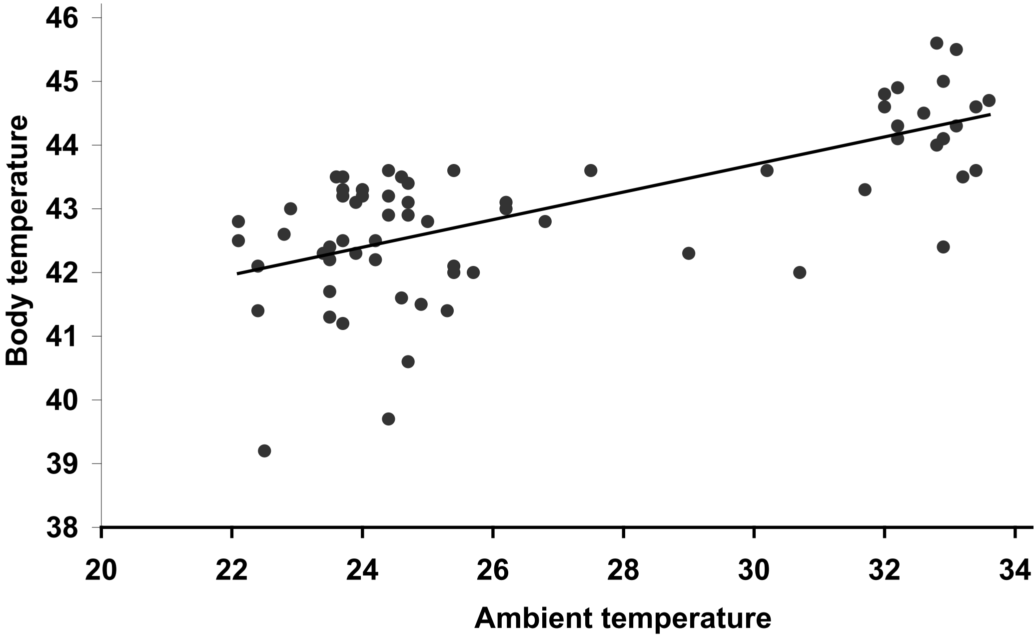

Figure 16. Relationship between ambient temperature (°C) in the shade and body temperature (°C) of 69 individual birds from 13 different species. Equation of the line: Body temperature = 37.2 + 0.22(ambient temperature); R2 = 0.45.

cost being the greater cost (Brown et al. 1994; Druce et al. 2006; Paper III), but this should not lead us to overlook the significance of metabolic costs.

Birds in hot environment may revert to the use of evaporative cooling to dissipate heat and avoid dehydration (Louw 1993), a process which is energetically expensive and promotes excessive water loss. Due to their high rates of metabolism, which is related to their high body temperatures (~ 41°C), birds tend to have a high rate of water loss. However birds inhabiting dry environments, possess adaptations to reduce the total evaporative water loss (TEWL) in order to conserve water (McNab 2002; Williams and Tieleman 2005). Such physiological adaptations include: a countercurrent heat exchange system in the nasal passages that can recover large amounts of water from exhaled air and reduce respiratory water loss (Tieleman et al. 1999; Sabat et al. 2006); alteration of the lipid composition in the skin (Menon et al. 1989; Williams and Tieleman 2005) as well as an increase in body temperature with ambient temperature i.e. the use of hyperthermia. Most studies on the use of hyperthermia to reduce energy costs and water loss in hot environments is, however confined to birds in laboratory settings (Tieleman & Williams 1999). In Paper V, we showed for the first time the use of hyperthermia by free ranging birds to reduce thermoregulatory costs (Fig. 16). Birds increased their body temperatures by up to 5 °C above normal temperatures when ambient temperatures were most likely above their upper critical temperature.

In Paper VI, captive birds avoided the thermally costly compartments at the beginning of the experiment when food availability was equal in all compartments. However, over the course of the day, they increased their use of the thermally expensive compartments, incurring a high thermoregulatory cost, probably due to declining food availability in the more favourable ambient compartment. They may have resorted to using costly physiological means to avoid overheating, while maintaining their energy intake. This implies that birds may alternate between the use of behavioral and physiological thermoregulation, depending on their internal state.

DIET SELECTION

An individual's diet selection strategy cannot be totally independent of its patch exploitation strategy (Heller 1980; Brown and Mitchell 1989). The original diet model assumed no depletion of resources and predicts no partial preferences among foods (Pulliam 1974). On the contrary, most studies on diet selection have shown situations where partial preferences occur as a result of optimal foraging, such as in the expanding specialist diet strategy (Heller 1980; Brown and Mitchell 1989). The expanding specialist strategy is that where a forager selectively harvests its preferred food i.e. the food with the higher profitability, until it is depleted to a critical level after which it expands its diet to include the less profitable food. The expansion point is determined by the density of the preferred food. Studies on seed selection in animals suggest that preference is mainly determined by handling times (Willson 1971) as well as seed distribution and densities (Brown and Mitchell 1989), while seed quality or chemical composition has mainly been overlooked. Seeds vary in their chemical composition e.g. in carbohydrates, proteins and lipids as well as in secondary compounds. However, seeds with higher concentrations of secondary compounds may not always be of low profitability (Pulliam 1980).

In my study on diet selection in birds (Paper IV), I investigated the diet selection strategy of birds feeding on two seed types, millet and peanut that differ both in energetic (Karasov and Martinez del Rio 2007) and toxic content (Odoemelam and Osu 2009). Results showed that birds employed the expanding specialist strategy, as they started by feeding selectively on peanuts but at some point became more selective towards millet (Fig. 17). Their expansion point however was determined by the amount of peanut seeds they had eaten, contrary to predictions. They took only ~1 g of peanut before switching to millet, irrespective of the amount of peanut left. In line with predictions on diet selection, preference for peanut may have been as a result of its higher profitability, since it contained more energy per gram than millet (Asibuo et al. 2008; Adeola and Orban 1995; Baryeh 2001) due to its high fat content. However, peanut contains a higher concentration of toxins than millet (Odoemelam and Osu 2009) and so, birds may be limited by how much of the toxins in peanuts they can handle which probably created a trade-off between energy gain and toxic exposure.

Birds may switch or expand their diet for several reasons ranging from increasing nutritional requirements e.g. for migration (McWilliams et al 2002) or breeding (Stutchbury and Morton 2001; Lahti 2003) to declining food availability (Dostine and Franklin 2002). They could also vary their diet composition to compensate for increased metabolic costs during harsh conditions (Whelan et al. 2000). Dry regions experience relatively high seasonal variation in temperatures, water and food availability (Walker 1985). Therefore the balance between metabolic water production and evaporative water loss may fluctuate and energetic or nutritional requirements may vary seasonally.

In my second experiment in Paper IV, I investigated a seasonal change in diet selection in birds. Generally birds preferred millet, however preference for millet decreased during the early wet season when background seed abundance must have declined (Dostine et al. 2001) and during this time more peanuts were taken. Even though grass seed availability was low, other food sources were readily available, e.g. insects, fruits etc. At this time, granivores may switch their diets to include other available foods (Dostine & Franklin 2002; Lahti 2003). Additionally, this was the breeding season for the main visitors to the feeding patches, village weavers, and they have been observed to include insects in their diets during this period (Lahti 2003; personal observation). Increased intake of peanuts was probably due to increasing nutritional demands during breeding.

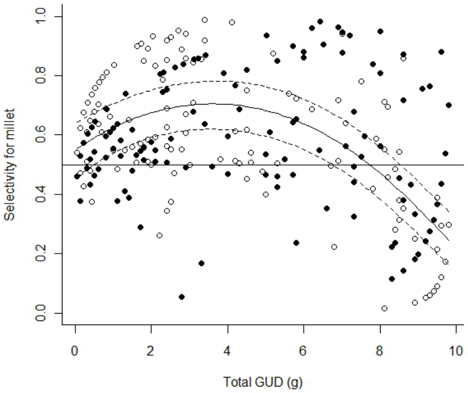

Figure 17. Selectivity index for millet as a function of total GUD (millet + peanut). The curve represents the prediction by the best model, which is the same for both patch types with different proportions of millet and peanut. Open circles represent low peanut patches and closed circles represent high peanut patches, with no difference in selectivity between patch types. Dashed curves represent 95 % confidence interval. The horizontal line represents the 0.5 mark, the region of equal or no selectivity. Above this line, millet is preferred and below the line peanut is preferred.

SUMMARY AND CONCLUSION

Measuring patch use by foragers (Brown 1988) reveals the magnitude and significance of the effects of the different costs associated with a foraging area. Hence it should be possible to use these behaviors as indicators of habitat quality and seasonal background food availability, as influenced by e.g. rainfall patterns. The behavior of foragers in artificial food patches will reflect significant temporal and spatial differences in the costs and benefits of foraging.

In this thesis, I have used the patch use behavior of birds as an indicator of a seasonal and environment-wide effect of food availability, water, predation risk and temperature. My studies have revealed to a great extent that the behavior observed among animals is shaped by the circumstances they are faced with in their environment. I show that while temporal (seasonal) variations in GUDs appear to be driven by food availability and water; small-scale spatial variation in GUDs seems to be driven by predation risk. Birds seem to be willing to trade-off food for thermoregulation (Tieleman and Williams 2002), however they may resort to more costly means of thermoregulation e.g. hyperthermia, when energy demand increases.

Proximity to drinking water seems to be a determinant of the extent to which granivorous birds will exploit their environment. This however appears to be tied to immediate environmental quality - when birds were offered some water, they depleted patches more when food availability was low, but less when there was plenty of food available. This has great implications for bird conservation. For example, increased foraging efficiency that could result from providing water in a degraded environment may adversely affect the overall productivity, through higher seed removal rates (Kotler et al. 1998). However this may not be a problem for good quality habitats.

My study supports the proposition that physiological considerations of diet selection be incorporated in ecological studies of food preferences (Whelan and Brown 2005; Whelan and Schmidt 2007). I further suggest that the quality of seeds may play a more important role than previously thought, in the diet selection strategy used by granivorous. Theoreticians may need to incorporate the effect of toxins rather than only considerations of seed densities in models of diet selection strategies. For birds that employ the expanding specialist strategy, when feeding on seeds that vary in toxic content, the expansion point may be dependent on how much toxin they can handle. Also, seasonal variation in diet as confirmed in many studies (see review by Whelan et al. 2000) may be related to changing nutritional requirements.

REFERENCES

Asibuo JY, Akromah R, Safo-Kantanka O, Adu-Dapaah HK, Ohemeng-Dapaah S and Agyeman A. (2008) Chemical composition of groundnut, Arachis hypogaea (L) landraces. Afr. J. Biotech. 7: 2203-2208.

Bacigalupe LD, Rezende EL, Kenagy GJ and Bozinovic F (2003) Activity and space use by degus: a trade-off between thermal conditions and food availability? J. Mammal. 84:311–318

Baryeh EA. (2001) Physical properties of millet. J. Food Eng. 51: 39–46.

Begon M, Harper JL and Townsend CR. (1996) Ecology. Blackwell Science Limited UK.

Bourliere F and Hadley M. (1970) The ecology of tropical savannas. Ann. Rev. Ecol. Syst. 1:125-152.

Bozinovic F and Vasquez RA. (1999) Patch use in a diurnal rodent: handling and searching under thermoregulatory costs. Funct. Ecol,. 13: 602–610.

Bozinovic F, Lagos JA, Vasquez RA and Kenagy GJ. (2000) Time and energy use under thermoregulatory constraints in a diurnal rodent. J. Therm. Biol. 25:251-256.

Brown JS. (1988) Patch use as an indicator of habitat preference, predation risk and competition. – Behav. Ecol. and Sociobiol., 22: 37–47.

Brown JS. (1992) Patch use under predation risk: I. Models and predictions. – Ann. Zool. Fenn., 29: 301–309.

Brown JS (2000) Foraging ecology of animals in response to heterogeneous environments. In: Hutchings MJ, John EA, Stewart AJA (eds) The ecological consequences of environmental heterogeneity. Blackwell Science, Oxford, pp 181-215.

Brown JS and Mitchell WA. (1989) Diet selection on depletable resources. Oikos 54:33-43.

Brown JS and Morgan RA. (1995) Effects of foraging behavior and spatial scale on diet selectivity: a test with fox squirrels. Oikos 74:122-136.

Brown JS and Kotler BP. (2004) Hazardous duty pay and the foraging cost of predation. – Ecol. Lett., 7:999-1014.

Brown JS, Kotler BP and Valone TJ (1994) Foraging under predation: a comparison of energetic and predation costs in rodent communities of the Negev and Sonoran deserts. Aust. J. Zool., 42:435-448.

Caraco T, Blanckenhorn WU, Gregory GM, Newman JA, Recer GR and Zwicker SM. (1990) Risk-sensitivity: ambient temperature affects foraging choice. Anim. Behav. 39:338-345.

Charnov EL. (1976) Optimal foraging: the marginal value theorem. Theor. Pop. Biol., 9: 129–136.

Crowley G and Garnett S. (1999) Seeds of the annual grasses Schizachyrium spp. as a food resource for tropical granivorous birds. Aust. J. Ecol. 24: 208–220.

Denlinger DL. (1980) Seasonal and annual variation of insect abundance in the Nairobi National Park, Kenya. Biotropica 12: 100-106.

Dostine PL and Franklin DC. (2002) A comparison of the diet of three finch species in the Yinberrie Hills area, Northern Territory. Emu 102: 159-164

Dostine PL, Johnson GC, Franklin DC, Zhang Y and Hempel C. (2001) Seasonal use of savanna landscapes by the Gouldian finch Erythrura gouldiae, in the Yinberrie Hills area, Northern Territory. Wildlife Research 28: 445-458.

Druce DJ, Brown JS, Castley JG, Kerley GH, Kotler BP, Slotow R and Knight MH (2006) Scale-dependent foraging costs: habitat use by rock hyraxes (Procavia capensis) determined using giving-up densities. Oikos 115: 513-525.

Emlen JM. (1966) The role of time and energy in food preference. Am. Nat. 100:611-617.

Ezealor AU. (2002) Critical Sites for Biodiversity Conservation in Nigeria. Nigerian Conservation Foundation.

Heller R. (1980) On optimal diet in a patchy environment. Theor. Pop. Biol. 17:201-214.

Hochman V and Kotler BP. (2006) Effects of food quality, diet preference and water on patch use by Nubian ibex. Oikos 112: 547-554.

Hopkins B. (1968) Vegetation of the Olokemeji Forest Feserve, Nigeria: V. the vegetation on the savanna site with special reference to its seasonal changes. J. Ecol. 56:97-115.

Houston AI, McNamara JM Hutchinson JMC. (1993) General results concerning the trade-off between gaining energy and avoiding predation. Phil. Trans. R. Soc. Lond. 341:375-397

Hutto RL. (1990) Measuring the availability of food resources. Stud. Avian Biol. 13: 20–28.

Karasov WH and Martinez del Rio C. (2007) Physiological Ecology: How Animals Process Energy, Nutrients, and Toxins. New Jersey: Princeton University Press.

Kenagy GJ, Vasquez RA, Barnes BM and Bozinovic F. (2004) Microstructure of summer activity bouts of Degus in a thermally heterogeneous habitat. J. Mammal. 85: 260-267.

Kilpatrick AM. (2003) The impact of thermoregulatory costs on foraging behavior: a test with American crows (Corvus brachyrhynchos) eastern grey squirrels (Sciurus carolinensis). Evol. Ecol. Res. 5: 781-786.

Kotler BP and Brown JS. (1990) Rates of seed harvest by two species of gerbilline rodents. J. Mammal. 71: 591-596.

Kotler BP, Dickman CR and Brown JS. (1998) The effects of water on patch use by two Simpson Desert granivores (Corvus coronoides and Pseudomys hermannsburgensis). Aust. J. Ecol. 23: 574-578.

Lahti DC. (2003) Cactus fruits may facilitate village weaver (Ploceus cucullatus) breeding in atypical habitat on Hispaniola. Wilson Bull. 115: 487–489.

Leisler B. (1992) Habitat selection and coexistence of migrants and Afrotropical residents. Ibis 134: 77-82.

Lilliendahl K, Carlson A, Welander J and Ekman JB. (1996) Behavioral control of daily fattening in great tits (Parus major). Can. J. Zool. 74:1612-1616.

Lima SL. (1985) Maximizing feeding efficiency and minimizing time exposed to predators: A trade-off in the black-capped chickadee. Oecologia.66: 60-67.

Louw G (1993) Physiological Animal Ecology. Longman, Essex.

MacArthur RH. and Pianka ER. (1966) On optimal use of a patchy environment. Am. Nat. 100: 603-609.

McNab BK. (2002) The physiological ecology of vertebrates: A view from energetic. Cornell University Press. Ithaca, New York.

McWilliams SR, Kearney SB and Karasov WH. (2002) Diet preferences of warblers for specific fatty acids in relation to nutritional requirements and digestive capabilities. J. Avian Biol. 33: 167–174.

Menon GK, Baptista LF, Brown BE and Elias PM. (1989) Avian epidermal differentiation. II. Adaptive response of permeability barrier to water deprivation and replenishment. Tissue Cell 21:83–92.

Molokwu MN, Olsson O, Nilsson J-Å and Ottosson U. 2008. Seasonal Variation in patch use in a tropical African environment. Oikos 117: 892-898. Manuscript nr. 1 in this thesis.

Molokwu MN, Nilsson J-Å, Ottosson U and Olsson O. (2010) Effects of season, water and predation risk on patch use by birds of an African savannah. Oecologia. doi: 10.1007/s00442-010-1781-3. Manuscript nr. 3 in this thesis.

Nix HA. (1983) Climate of tropical savanna. In: Bourliere F (ed) Ecosystems of the world: Tropical savannas. Elsevier scientific publishing company, Amsterdam, pp 37-62.

Nolet BA, Fulf VN and van Rijswijk MEC. (2006) Foraging costs and accessibility as determinants of giving-up densities in a swan-pondweed system. Oikos 112: 353-362.

Odoemelam SA and Osu CI. 2009. Evaluation of the phytochemical cintent of some edible grains marketed in Nigeria. E-Journal of Chemistry 6: 1193–1199.

Olsson O and Holmgren NMA. (1999) The survival-rate-maximizing policy for Bayesian foragers: wait for good news. Behav. Ecol. 9:345-353.

Olsson O and Molokwu MN. (2007) On the missed opportunity cost, GUD, and estimating environmental quality. Isr. J. Ecol. Evol. 53: 263-278. Manuscript nr. 2 in this thesis.

Olsson O, Brown JS and Smith HG. (2002) Long- and short- term state-dependent foraging under predation risk: an indication of habitat quality. Anim. Behav. 63: 981–989.

Olsson O, Wiktander U and Malmqvist A. (2001) Variability of patch type preferences in relation to resource availability and breeding success in a bird. – Oecologia, 127: 435–443.

Olsson O, Wiktander U, Holmgren NMA and Nilsson SG. (1999) Gaining ecological information about Bayesian foragers through their behavior. II. A field test with woodpeckers. Oikos, 87: 264-276.

Oyugi JO and Brown JS. (2003) Giving-up densities and habitat preferences of European starlings and American robins. Condor 105:130-135.

Payne RB. (1998) A new species of firefinch Lagonosticta from northern Nigeria and its association with the Jos Plateau Indigobird Vidua maryae. Ibis 140: 368-381.

Persson A and Stenberg M. (2006) Linking patch-use behavior, resource density, and growth expectations in fish. Ecology 87: 1953-1959.

Pulliam HR. (1974) On the theory of optimal diets. Am. Nat. 108:59-74.

Pulliam HR. 1980. Do chipping sparrows forage optimally? Ardea 68: 75–82.

Pyke GH. (1984) Optimal foraging theory: a critical review. Ann. Rev. Ecol. Syst. 15: 523-575.

Rosenzweig ML. (2007) On foraging theory, humans and the conservation of diversity: A prospectus. In Stephens DW, Brown JS and Ydenberg RC (eds) Foraging: Behaviour and Ecology. The University of Chicago Press. Chicago, pp 483-501.

Sabat P, Cavieres G, Veloso C and Canals M. (2006) Water and energy economy of an omnivorous bird: Population differences in the Rufous-collared Sparrow (Zonotrichia capensis). Comp. Biochem. Physiol. 144:485-490

Schmidt-Nielsen K. (1997) Animal Physiology: Adaptation and Environment. Cambridge University Press. Cambridge.

Shrader AM, Kotler BP, Brown JS and Kerley GIH. (2008) Providing water for goats in arid landscapes: effects on feeding effort with regard to time period, herd size and secondary compounds. Oikos 117: 466-472.

Sih A and Christensen B. (2001) Optimal diet theory: when does it work, and when and why does it fail? Anim. Behav. 61:379-390.

Stephens DW and Krebs JR (1986) Foraging Theory. Princeton University Press, New Jersey.

Stephens DW, Brown JS and Ydenberg RC, ed. (2007) Foraging: Behaviour and Ecology. The University of Chicago Press. Chicago.

Stutchbury BJM and Morton ES. (2001) Behavioral ecology of tropical birds. Academic Press, London.

Tieleman BI and Williams JB. (1999) The role of hyperthermia in the water economy of desert birds. Physiol.Biochem. Zool. 72: 87-100.

Tieleman BI and Williams JB. (2002). Effects of food supplementation on behavioral decisions of hoopoe-larks in the Arabian Desert: balancing water, energy and thermoregulation. Anim. Behav. 63: 519-529.

Van Gils JA, De Rooij SR, Van Belle J, Van der Meer J, Dekinga A, Piersma T and Drent R. (2005) Digestive bottleneck affects foraging decisions in red knots Calidris canutus. I. Prey choice. J. Anim. Ecol. 74:105-119.

Walker BH. (1985) Structure and function of savannas: an overivew. In Tothill JC, Mott JJ (eds) Ecology and management of the world's savannas. Commonwealth Agricultural Bureaux, pp 83-91.

Walsberg GE. (1983) Ecological energetic: what are the questions? In; Perspectives of Ornithology. Cambridge University Press. Cambridge, pp 135-164

Werner EE and Hall DJ. (1974) Optimal foraging and the size selection of prey by the bluegill sunfish (Lepomis macrochirus). Ecology 55:1042-1052.

Whelan CJ and Brown JS. (2005) Optimal foraging and gut constraints: reconciling two schools of thought. Oikos 110:481-496.

Whelan CJ and Jedlicka DM. (2007) Augmenting population monitoring programs with behavioral indicators during ecological restorations. Israel J. Ecol.Evol. 53:279-295.

Whelan CJ and SchmidtKA. (2007) Food acquisition, processing and digestion. In

Stephens DW, Brown JS and Ydenberg RC (eds) Foraging: Behaviour and Ecology. The University of Chicago Press. Chicago, pp 141-172.

Whelan CJ, Brown JS, Schmidt KA, Steele BB and Willson ME. (2000) Linking consumer-resource theory and digestive physiology: Application to diet shifts. Evol. Ecol. Res. 2: 911-934.

Williams JB and Tieleman BI. (2005) Physiological adaptation in desert birds. BioScience 55 416-425.

Willson ME. 1971. Seed selection in some North American finches. Condor 73: 415–429.

Ydenberg RC, Brown JS and Stephens DW. (2007) Foraging: An overview. In Stephens DW, Brown JS and Ydenberg RC (eds) Foraging: Behaviour and Ecology. The University of Chicago Press. Chicago, pp 1-28.

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I appreciate late **Mr Joseph Okafor, Mrs Uka Okafor** and family. Thank you for your kindness and support throughout these years.

I thank **Mr and Mrs P.C. Molokwu, Amaka, Cynthia, Peter** and **Maurice** for providing me with a home away from home in Jos. Thanks for your kindness.

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Last but far from the least, I thank and appreciate greatly my family; **daddy, mummy, Ogo** and **Emeke**. Your encouragement and prayers kept me going all these years. Thanks for your love and support. Despite being so far away I feel the bond has grown even stronger. I love you all deeply.

The following is a list of Doctoral theses (Lund University,Sweden) from the Department of Animal Ecology (nos. 1-78, from no. 79 and onwards denoted by (A)) and Theoretical Ecology (T). (E) refers to Doctoral theses from the Department of Chemical Ecology/Ecotoxicology during the years 1988-1995.

1. CHARLOTTE HOLMQVIST. Problem on marine-glacial relicts on account on the genus Mysis. 6 May 1959.
2. HANS KAURI. Die Rassenbildung bei europäischen Rana-Arten und die Gültigkeit der Klimaregeln. 9 May 1959.
3. PER DALENIUS. Studies on the Oribatei (Acari) of the Torneträsk territory in Swedish Lapland. 14 May 1963.
4. INGEMAR AHLÉN. Studies on the history of distribution, taxonomy and ecology of the Red Deer in Scandinavia. 21 May 1965.
5. STAFFAN ULFSTRAND. Bentic animal communities of river Vindelälven in Swedish Lapland. 8 May 1968.
6. SAM ERLINGE. Food habits, home range and territoriality of the otter Lutra lutra L. 6 May 1969.
7. GUNNAR MARKGREN. Reproduction of moose in Sweden. 17 May 1969.
8. ARNE BERGENGREN. On genetics, evolution and history of the heath-hare, a distinct population of the arctic hare, Lepus timidus L. 17 October 1969.
9. HåKAN HALLANDER. Habitats and habitat selection in the wolf spiders Pardosa chelata (O.F. Müller) and P. pullata (Clerck). 20 March 1970.
10. ULF SCHELLER. The Pauropoda of Ceylon. 29 May 1970.
11. LEIF NILSSON. Non-breeding ecology of diving ducks in southernmost Sweden. 2 December 1970.
12. RUNE GERELL. Distributional history, food habits, diel behaviour, territoriality, and population fluctuations of the mink Mustela vison Schreber in Sweden. 30 March 1971.
13. INGRID HANSSON. Skull nematodes in mustelids. 3 June 1971.
14. STURE ABRAHAMSSON. Population ecology and relation to environmental factors of Astacus astacus Linné and Pacifastacus leniusculus Dana. 3 June 1971.
15. LENNART HANSSON. Food conditions and population dynamics of Scandinavian granivorous and herbivorous rodents. 26 November 1971.
16. SVEN-AXEL BENGTSON. Ecological segregation, reproduction and fluctuations in the size of duck populations in Iceland. 21 April 1972.
17. STEN ANDREASSON. Distribution, habitat selection, food and diel activity

of Swedish freshwater sculpins (Cottus L.). 5 May 1972.

18. KERSTIN SVAHN. Coccidian blood parasites in Lacertids. 17 May 1972.
19. RUTGER ROSENBERG. Macrofaunal recovery in a Swedish fjord following the closure of a sulphite pulp mill. 13 April 1973.
20. SVEN ALMQVIST. Habitat selection and spatial distribution of spiders in coastal sand dunes. 25 May 1973.
21. TORSTEN MALMBERG. Population fluctuations and pesticide influence in the rook Corvus
frugilegus L., in Scania, Sweden 1955-1970. 25 May 1973.
22. ANDERS SÖDERGREN. Transport, distribution, and degradation of organochlorine residues in limnic ecosystems (defended at the Dept of Limnology). 23 May 1973.
23. BERITH PERSSON. Effects of organochlorine residues on the whitethroat Sylvia communis Lath. 7 December 1973.
24. PLUTARCO CALA. The ecology of the ide Idus idus (L.) in the river Kävlingeån, South Sweden. 23 May 1975.
25. ÅKE GRANMO. Effects of surface active agents on marine mussels and fish. 26 May 1975.
26. BO W SVENSSON. Population ecology of adult Potamophylax cingulatus (Steph.) and other
Trichoptera at a South Swedish stream. 15 October 1975.
27. STEN NORDSTRÖM. Associations, activity, and growth in lumbricids in southern Sweden. 6 April 1976.
28. STEN RUNDGREN. Environment and lumbricid populations in southern Sweden. 8 April 1976.
29. CHRISTIAN OTTO. Energetics, dynamics and habitat adaptation in a larval population of Potamophylax cingulatus (Steph.) (Trichoptera). 9 April 1976.
30. JAN LÖFQVIST. The alarm-defence system in formicine ants. 21 May 1976.
31. LARS HAGERMAN. Respiration, activity and salt balance in the shrimp Crangon vulgaris (Fabr.). 22 October 1976.
32. THOMAS ALERSTAM. Bird migration in relation to wind and topography. 29 October 1976.
33. LARS M NILSSON. Energetics and population dynamics of Gammarus pulex L. Amphipoda. 20 December 1977.
34. ANDERS NILSSON. Ticks and their small mammal hosts. 24 May 1978.
35. SÖREN SVENSSON. Fågelinventeringar - metoder och tillämpningar. (Bird censuses - methods and applications.) 23 May 1979.

36. BO FRYLESTAM. Population ecology of the European hare in southern Sweden. 1 June 1979.
37. SVEN G NILSSON. Biologiska samhällen i heterogena miljöer: En studie på fastland och öar. (Biological communities in heterogeneous habitats: A study on the mainland and islands.)
12 October 1979.
38. BJÖRN SVENSSON. The association between Epoicocladius flavens (Chironomidae) and Ephemera danica (Ephemeroptera). 26 October 1979.
39. GÖRAN HÖGSTEDT. The effect of territory quality, amount of food and interspecific competition on reproductive output and adult survival in the magpie Pica pica; an experimental study. 29 February 1980.
40. JON LOMAN. Social organization and reproductive ecology in a population of the hooded crow Corvus cornix. 9 April 1980.
41. GÖRGEN GÖRANSSON. Dynamics, reproduction and social organization in pheasant Phasianus colchicus populations in South Scandinavia. 26 September 1980.
42. TORSTEN DAHLGREN. The effects of population density and food quality on reproductive output in the female guppy, Poecilia reticulata (Peters). 27 February 1981.
43. AUGUSTINE KORLI KORHEINA. Environments and co-existence of Idotea species in the southern Baltic. 15 May 1981.
44. INGVAR NILSSON. Ecological aspects on birds of prey, especially long-eared owl and tawny owl. 9 October 1981.
45. TORBJÖRN von SCHANTZ. Evolution of group living, and the importance of food and social organization in population regulation; a study on the red fox (Vulpes vulpes). 23 October 1981.
46. OLOF LIBERG. Predation and social behaviour in a population of domestic cat. An evolutionary perspective. 11 December 1981.
47. BJÖRN MALMQVIST. The feeding, breeding and population ecology of the brook lamprey (Lampetra planeri). 12 March 1982.
48. INGVAR WÄREBORN. Environments and molluscs in a non-calcareous forest area in southern Sweden. 19 March 1982.
49. MAGNUS SYLVÉN. Reproduction and survival in common buzzards (Buteo buteo) illustrated by the seasonal allocation of energy expenses. 26 March 1982.
50. LARS-ERIC PERSSON. Structures and changes in soft bottom communities in the southern Baltic. 23 April 1982.
51. GÖRAN BENGTSSON. Ecological significance of amino acids and metal ions,

a microanalytical approach. 24 May 1982.

52. JAN HERRMANN. Food, reproduction and population ecology of Dendrocoelum lacteum (Turbellaria) in South Sweden. 10 December 1982.
53. BO EBENMAN. Competition and differences in niches and morphology between individuals, sexes and age classes in animal populations, with special reference to passerine birds. 8 April 1983.
54. HANS KÄLLANDER. Aspects of the breeding biology, migratory movements, winter survival, and population fluctuations in the great tit Parus major and the blue tit P. caeruleus. 29 April 1983.
55. JOHNNY KARLSSON. Breeding of the starling (Sturnus vulgaris). 6 May 1983.
56. CARITA BRINCK. Scent marking in mustelids and bank voles, analyses of chemical compounds and their behavioural significance. 17 May 1983.
57. PER SJÖSTRÖM. Hunting, spacing and antipredatory behaviour in nymphs of Dinocras cephalotes (Plecoptera). 1 June 1983.
58. INGE HOFFMEYER. Interspecific behavioural niche separation in wood mice (Apodemus flavicollis and A. sylvaticus) and scent marking relative to social dominance in bank voles (Clethrionomys glareolus). 9 December 1983.
59. CHRISTER LÖFSTEDT. Sex pheromone communication in the turnip moth Agrotis segetum. 30 November 1984.
60. HANS KRISTIANSSON. Ecology of a hedgehog Erinaceus europaeus population in southern Sweden. 7 December 1984.
61. CHRISTER BRÖNMARK. Freshwater molluscs: Distribution patterns, predation and interactions with macrophytes. 19 April 1985.
62. FREDRIK SCHLYTER. Aggregation pheromone system in the spruce bark beetle Ips typographus. 26 April 1985.
63. LARS LUNDQVIST. Life tactics and distribution of small ectoparasites (Anoplura, Siphonaptera and Acari) in northernmost Fennoscandia. 10 May 1985.
64. PEHR H ENCKELL. Island life: Agency of Man upon dispersal, distribution, and genetic variation in Faroese populations of terrestrial invertebrates. 3 June 1985.
65. SIGFRID LUNDBERG. Five theoretical excursions into evolutionary ecology: on coevolution, pheromone communication, clutch size and bird migration. 7 November 1985.
66. MIKAEL SANDELL. Ecology and behaviour of the stoat Mustela erminea and a theory on delayed implantation. 8 November 1985.

67. THOMAS JONASSON. Resistance to frit fly attack in oat seedlings, and ecological approach to a plant breeding problem. 13 November 1985.
68. ANDERS TUNLID. Chemical signatures in studies of bacterial communities. Highly sensitive and selective analyses by gas chromatography and mass spectrometry. 3 October 1986.
69. BOEL JEPPSSON. Behavioural ecology of the water vole, Arvicola terrestris, and its implication to theories of microtine ecology. 27 May 1987.
70. TORSTEN GUNNARSSON. Soil arthropods and their food: choice, use and consequences. 2 June 1987.
71. THOMAS MADSEN. Natural and sexual selection in grass snakes, Natrix natrix, and adders, Vipera berus. 4 September 1987.
72. JENS DAHLGREN. Partridge activity, growth rate and survival: Dependence on insect abundance. 4 December 1987.
73. SCOTT GILBERT. Factors limiting growth of sympatric Peromyscus and Clethrionomys populations in northern Canada. 11 December 1987.
74. OLLE ANDERBRANT. Reproduction and competition in the spruce bark beetle Ips typographus. 8 April 1988.
75. EINAR B OLAFSSON. Dynamics in deposit-feeding and suspension-feeding populations of the bivalve Macoma baltica; an experimental study. 29 April 1988.
76. JAN-ÅKE NILSSON. Causes and consequences of dispersal in marsh tits, time as a fitness factor in establishment. 11 May 1988.
77. PAUL ERIC JÖNSSON. Ecology of the southern Dunlin Calidris alpina schinzii. 13 May 1988.
78. HENRIK G SMITH. Reproductive costs and offspring quality: the evolution of clutch size in tits (Parus). 20 May 1988.
79. BILL HANSSON. (A) Reproductive isolation by sex pheromones in some moth species. An electrophysiological approach. 14 October 1988.
80. ANDERS THURÉN. (E) Phthalate esters in the environment: analytical methods, occurrence, distribution and biological effects. 4 November 1988.
81. KARIN LUNDBERG. (A) Social organization and survival of the pipistrelle bat (Pipistrellus pipistrellus), and a comparison of advertisement behaviour in three polygynous bat species. 10 February 1989.
82. HAKON PERSSON. (A) Food selection, movements and energy budgets of staging and wintering geese on South Swedish farmland. 6 December 1989.
83. PETER SUNDIN. (E) Plant root exudates in interactions between plants and soil micro-organisms. A gnotobiotic approach. 16 March 1990.

84. ROLAND SANDBERG. (A) Celestial and magnetic orientation of migrating birds: Field experiments with nocturnal passerine migrants at different sites and latitudes. 28 September 1990.
85. ÅKE LINDSTRÖM. (A) Stopover ecology of migrating birds. 12 October 1990.
86. JENS RYDELL. (A) Ecology of the northern bat Eptesicus nilssoni during pregnancy and lactation. 26 October 1990.
87. HÅKAN WITTZELL. (T) Natural and sexual selection in the pheasant Phasianus colchicus. 27 September 1991.
88. MATS GRAHN. (A) Intra- and intersexual selection in the pheasant Phasianus colchicus. 27 May 1992.
89. ANN ERLANDSSON. (A) Life on the water surface: behaviour and evolution in semiaquatic insects. 25 September 1992.
90. GUDMUNDUR A GUDMUNDSSON. (A) Flight and migration strategies of birds at polar latitudes. 2 October 1992.
91. IO SKOGSMYR. (T) Pollination biology, venereal diseases and allocation conflicts in plants. 9 October 1992.
92. ANDERS VALEUR. (E) Utilization of chromatography and mass spectrometry for the estimation of microbial dynamics. 16 October 1992.
93. LENA TRANVIK . (A) To sustain in a stressed environment: a study of soil Collembola. 27 November 1992.
94. KATARINA HEDLUND. (A) Animal-microbial interactions: The fungivorous Collembola.

12 February 1993.

95. HANS EK. (E) Nitrogen acquisition, transport and metabolism in intact ectomycorrhizal associations studied by 15N stable isotope techniques.14 May 1993.
96. STAFFAN BENSCH. (A) Costs, benefits and strategies for females in a polygynous mating system: a study on the great reed warbler. 24 September 1993.
97. NOÉL HOLMGREN. (T) Patch selection, conflicting activities and patterns of migration in birds.15 October 1993.
98. ROLAND LINDQUIST. (E) Dispersal of bacteria in ground water - mechanisms, kinetics and consequences for facilitated transport. 3 December 1993.
99. JOHAN NELSON. (A) Determinants of spacing behaviour, reproductive success and mating system in male field voles, Microtus agrestis. 20 May 1994.
100. MARIA SJÖGREN. (A) Dispersal in and ecto-mycorrhizal grazing by soil invertebrates. 30 September 1994.

101. DENNIS HASSELQUIST. (A) Male attractiveness, mating tactics and realized fitness in the polygynous great reed warbler. 14 October 1994.
102. DORETE BLOCH. (A) Pilot whales in the North Atlantic. Age, growth and social structure in Faroese grinds of long-finned pilot whale, Globicephala melas. 16 December 1994.
103. MAGNUS AUGNER. (T) Plant-plant interactions and the evolution of defences against herbivores. 10 February 1995.
104. ALMUT GERHARDT. (E). Effects of metals on stream invertebrates. 17 February 1995.
105. MARIANO CUADRADO. (A) Site fidelity and territorial behaviour of some migratory passerine species overwintering in the Mediterranean area. 31 March 1995.
106. ANDERS HEDENSTRÖM. (T) Ecology of Avian Flight. 7 April 1995.
107. OLOF REGNELL. (E) Methyl mercury in lakes: factors affecting its production and partitioning between water and sediment. 21 April 1995.
108. JUNWEI ZHU. (A) Diversity and conservatism in moth sex pheromone systems. 4 May 1995.
109. PETER ANDERSON. (A) Behavioural and physiological aspects of oviposition deterrence in moths. 12 May 1995.
110. JEP AGRELL. (A) Female social behaviour, reproduction and population dynamics in a non-cyclic population of the field vole (Microtus agrestis).19 May1995.
111. SUSANNE ÅKESSON. (A) Avian Migratory Orientation: Geographic, Temporal and Geomagnetic Effects. 22 September 1995.
112. ADRIAN L. R. THOMAS. (A) On the Tails of Birds. 29 September 1995.
113. WENQI WU.(A) Mechanisms of specificity in moth pheromone production and response. 8 December 1995.
114. PER WOIN.(E) Xenobiotics in Aquatic Ecosystems: Effects at different levels of organisation. 15 December 1995.
115. K. INGEMAR JÖNSSON. (T) Costs and tactics in the evolution of reproductive effort. 12 April 1996.
116. MATS G.E. SVENSSON. (A) Pheromone-mediated mating system in a moth species. 30 October 1996.
117. PATRIC NILSSON. (T) On the Ecology and Evolution of Seed and Bud Dormancy. 9 May 1997.
118. ULF OTTOSSON. (A) Parent-offspring relations in birds: conflicts and trade-offs. 16 May 1997.

119. ERIK SVENSSON. (A) Costs, benefits and constraints in the evolution of avian reproductive tactics: a study on the blue tit. 6 June 1997.
120. MARIA SANDELL. (A). Female reproductive strategies and sexual conflicts in a polygynous mating system. 6 March 1998.
121. ULF WIKTANDER. (A) Reproduction and survival in the lesser spotted woodpecker. Effects of life history, mating system and age. 3 April 1998.
122. OLA OLSSON. (A) Through the eyes of a woodpecker: understanding habitat selection, territory quality and reproductive decisions from individual behaviour. 17 April 1998.
123. PETER VALEUR. (A) Male moth behaviour and perception in the pheromone plums. 24 April 1998.
124. LARS PETTERSSON. (A) Phenotypic plasticity and the evolution of an inducible morphological defence in crucian carp. 19 March 1999.
125. JOHANNES JÄREMO. (T) Plant inducible responses to damage: evolution and ecological implications. 23 April 1999.
126. ÅSA LANGEFORS. (A) Genetic variation in Mhc class IIB in Atlantic Salmon: Evolutionary and Ecological Perspectives. 10 September 1999.
127. NILS KJELLÉN. (A) Differential migration in raptors. 12 November 1999.
128. ANDERS NILSSON. (A) Pikeivory: behavioural mechanisms in northern pike piscivory. 14 January2000.
129. JÖRGEN RIPA. (T) Population and community dynamics in variable environments. 21 January 2000.
130. BJÖRN LARDNER. (A) Phenotypic plasticity and local adaptation in tadpoles. 28 April 2000.
131. IRENE PERSSON. (A) Parental and embryonic behaviours in precocial birds. 19 May 2000.
132. ROGER HÄRDLING. (T) Evolutionary resolutions of conflicts with mates and offspring. 6 October 2000.
133. ÅSA LANKINEN. (T) Pollen competition as a target for sexual selection in plants. 17 November 2000.
134. THOMAS OHLSSON. (A) Development and maintenance of quality indicators in pheasants. 15 December 2000.
135. ANDERS KVIST. (A) Fuelling and flying: adaptations to endurance exercise in migrating birds. 20 April 2001.
136. ANNA-KARIN AUGUSTSSON. (A). On enchytraeids and naidids: Life-history traits and response to environmental stress. 23 May 2001.
137. MARIO PINEDA. (T). Evolution in Multicellular Mitotic Lineages. 31 August

2001.

138. LIV WENNERBERG. (A). Genetic variation and migration of waders. 9 November 2001
139. NICLAS JONZÉN. (T). Inference and management of populations in variable environments. 14 December 2001.
140. DAGMAR GORMSEN. (A). Colonization processes of soil fauna and mycorrhizal fungi. 21 December 2001.
141. PETER FRODIN. (T). Species interactions and community structure. 15 Mars 2002.
142. JOHAN BÄCKMAN (A). Bird Orientation: External Cues and Ecological Factors. 26 April 2002.
143. MÅNS BRUUN. (A). On starlings and farming: population decline, foraging strategies, cost of reproduction and breeding success. 7 June 2002.
144. JAKOB LOHM. (A). MHC and genomic diversity in Atlantic salmon (Salmo salar L.) 11 October 2002.
145. LARS RÅBERG. (A). Costs in ecology and evolution of the vertebrate immune system. 18 October 2002.
146. HELENE BRACHT JÖRGENSEN. (A). Food selection and fitness optimisation in insects. 13 December 2002.
147. MARTIN GREEN. (A). Flight strategies in migrating birds: when and how to fly. 31 January 2003.
148. BENGT HANSSON (A). Dispersal, inbreeding and fitness in natural populations. 21 February 2003.
149. MIKAEL ROSÉN. (A). Birds in the flow: Flight mechanics, wake dynamics and flight performance. 11 April 2003.
150. JONAS HEDIN. (A). Metapopulation ecology of Osmoderma eremita - dispersal, habitat quality and habitat history. 23 May 2003.

151 HELENA WESTERDAHL. (A). Avian MHC: variation and selection in the wild. 10 October 2003.

152. KEN LUNDBORG. (T). Food hoarding: Memory and social conditions - an evolutionary approach. 16 January 2004.
153. RICHARD OTTVALL (A). Population ecology and management of waders breeding on coastal meadows. 19 February 2004.
154. RACHEL MUHEIM (A). Magnetic Orientation in Migratory Birds. 20 February 2004.
155. MARIA HANSSON (A). Evolution and ecology of AhR genes in Atlantic salmon (Salmo salar L.). 23 April 2004.

156. MARTIN STJERNMAN (A). Causes and consequences of blood parasite infections in birds. 29 October 2004.
157. MARTIN GRANBOM (A). Growth conditions and individual quality in starlings. 19 November 2004.
158. ANNA GÅRDMARK (T). Species interactions govern evolutionary and ecological effects of population harvesting. 27 May 2005.
159. JONAS WALDENSTRÖM (A). Epidemiology and population structure of Campylobacter jejuni and related organisms in wild birds. 2 December 2005.
160. HELEN IVARSSON (T). Strategy Games: on survival and reproduction. 9 December 2005.
161. SEBASTIAN TROËNG (A). Migration of sea turtles from Caribbean Costa Rica: Implications for management. 14 December 2005.
162. EMMA SERNLAND (T). Optimal strategies and information in foraging theory. 16 December 2005.
163. MIKAEL ÅKESSON (A). Quantitative genetics and genome structure in a wild population: the use of a great reed warbler pedigree. 29 September 2006.
164. LENA MÅNSSON (T). Understanding weather effects on, in and from large herbivore population dynamics. 13 October 2006.
165. ERIK ÖCKINGER (A). Butterfly diversity and dispersal in fragmented grasslands. 17 November 2006.
166. JESSICA K. ABBOTT (A). Ontogeny and population biology of a sex-limited colour polymorphism. 23 November 2006.
167. OLOF HELLGREN (A). Avian malaria and related blood parasites: molecular diversity, ecology and evolution. 15 December 2006.
168. ANNA NILSSON (A).The problem of partial migration - the case of the blue tit. 19 January 2007.
169. PATRIK KARLSSON NYED (T). Food webs, models and species extinctions in a stochastic environment. 16 February 2007.
170. MARKUS FRANZÉN (A). Insect Diversity in Changing Landscapes. 16 May 2007.
171. MAJ RUNDLÖF (A). Biodiversity in agricultural landscapes: landscape and scale-dependent effects of organic farming. 15 June 2007.
172. OSKAR BRATTSTRÖM (A). Ecology of red admiral migration. 21 September 2007.
173. MICHAEL TOBLER (A). Maternal programming: costs, benefits and constraints of maternal hormone transfer. 5 October 2007.
174. FREDRIK HAAS (T). Hybrid zones and speciation - insights from the European

Crow hybrid zone. 25 January 2008.

175. JACOB JOHANSSON (T). Evolving ecological communities in changing environment. 1 February 2008.
176. THOMAS GOSDEN (A). The Preservation of Favoured Morphs in the Struggle Between Sexes. 29 May 2008.
177. ROINE STRANDBERG (A). Migration strategies of raptors – spatio-temporal adaptions and constraints in travelling and foraging. 24 September 2008.
178. SARA S. HENNINGSSON (A). On the role of migration for the distribution of arctic birds – a circumpolar perspective. 25 September 2008.
179. JONAS KNAPE (T). Population dynamics and demography – inference from stochastic models. 6 February 2009.
180. NICLAS NORRSTRÖM (T). Artificial neural networks in models of specialization and sympatic speciation. 20 February 2009.
181. JOHAN NILSSON (A). Causes and consequences of individual variation in energy turnover rates. 17 April 2009.
182. MARTA WOLF (T). Catching the Invisible: Aerodynamic Track and Kinematics of Bat and Bird Flight. 14 May 2009.
183. JULIANA DÄNHARDT (A). On the importance of farmland as stopover habitat for migrating birds. 15 May 2009.
184. SARA NAURIN (A). Avian GEnome Evolution – Gene Expression, Gene Divergence and Sexual Dimorphism. 23 October 2009.
185. JENNIE NILSSON (T). On the origin of polymorphism – consequences of competition and predation in heterogeneous environments. 13 November 2009.
186. FABRICE EROUKHMANOFF (A). The interplay between selection and constraints on phenotypic evolution and adaptive divergence. 20 November 2009.
187. SANNA HARRIS (A). Behaviour under predation risk – antipredator strategies, behavioural syndromes and sex-specific responses in aquatic prey. 15 January 2010.
188. PER HENNINGSSON (T). Always on the wing – Fluid dynamics, flight performance and flight behavior of common swifts. 29 Januari 2010.
189. HÅKAN KARLSSON (A). There and Back Again - Nocturnal migratory behaviour of birds during spring and autumn. 8 October 2010.
190. MARY NGOZI MOLOKWU (A). Costs of foraging in a dry tropical environment. 29 October 2010.

I Molokwu M.N., Olsson O., Nilsson J-Å. and Ottosson U. (2008) Seasonal variation in patch use in a tropical African environment. Oikos 117: 892-898.

II Olsson O. and Molokwu M.N. (2007) On the missed opportunity cost, GUD and estimating environmental quality. Isreal Journal of Ecology and Evolution 53:263-278.

III Molokwu M.N., Nilsson J-Å., Ottosson U., and Olsson O (2010) Effects of season, water and predation risk on patch use by birds of an African savannah. Oecologia. doi: 10.1007/s00442-010-1781-3.

IV Molokwu M.N., Nilsson J-Å., and Olsson O. Diet selection in birds: trade-off between energetic content and other qualities of seeds. Submitted.

V Nilsson J-Å., Molokwu M.N. and Olsson O. The use of hyperthermia in hot environments. Manuscript.

VI Molokwu M.N., Nilsson J-Å., Onoja J.D. and Olsson O. Effects of temperature on food intake in savannah birds. Manuscript.

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