GENERAL INTRODUCTION AND OUTLINE OF THE STUDY

Energy is essential for metabolic processes, activity, growth and reproduction of all animals. Thus, animal survival and fitness greatly depend on the regulation of energy intake. It is therefore not surprising that a comprehensive literature has focused on the foraging behaviour of animals that underlies energy and nutrient intake. Optimal foraging theories predict that animal fitness depends on the efficiency of foraging, and that animals forage so as to maximize their fitness (Pyke et al. 1977).

When the nutrient or energy content of a food source is low, animals ingest larger amounts. This is commonly known as compensatory feeding, and can be observed in various animal taxa (Karasov and Martínez del Rio 2007). Animals also increase their food intake after periods of food deprivation to compensate for an energy deficit (Zubair and Leeson 1996). When energy demands increase, such as during exercise, reproduction or cold exposure, food intake is also increased (Starck 1999). This compensation for low food quality, food deprivation or high energy requirements has been demonstrated in insects, fish, reptiles, birds and mammals. The widespread distribution of the compensatory feeding response demonstrates the importance of the regulation of energy intake for animal survival and fitness.

The energy that animals gain from their food, however, is determined not only by their foraging decisions, but also by the digestive processing of food. The macronutrients (carbohydrates, proteins and lipids) present in ingested food need to be broken down into their smallest components, a process that involves numerous enzymatic pathways. The breakdown products are subsequently absorbed by the epithelium of the gastrointestinal tract, either passively by diffusion or actively via carrier-mediated mechanisms (Karasov and Martínez del Rio 2007). The rate at which nutrients are ingested and digested under maintenance conditions can be increased when the animal experiences energetically challenging conditions. The difference between nutrient intake rate for maintenance and maximal nutrient intake rate is termed spare digestive capacity (Karasov and McWilliams 2005). However, the increase in food intake is limited by the volumetric capacity of the intestine or the rate at which food is broken down (Karasov and McWilliams 2005). To overcome these physiological constraints, the gastrointestinal tract of many vertebrates shows morphological flexibility: its size and structure can be adjusted according to food quality and availability, and energy requirements (Starck 1999). Animals that experience increased energy demands and unpredictable variations in food supply, such as birds during migration, can increase their energy intake by increasing their intestinal size (McWilliams and Karasov 2001). Partial atrophy of the intestine, on the other hand, may save energy during periods of food restriction (McWilliams and Karasov 2001; Ott and Secor 2007). Such changes in gut size can occur rapidly, especially in small animals, and one must carefully distinguish between acute and long-term spare capacities of an animal (Karasov and McWilliams 2005).

In addition to experimental studies of animal digestive performances, mathematical models have provided insight into the efficiency of energy and nutrient extraction from food. Penry and Jumars (1986) were the first to compare digestive processes to principles of chemical-reactor theory. As in a chemical reactor, the performance of animal intestines can be estimated from nutrient conversion efficiency, reaction time, digesta retention time, intestinal volume and the flow rate of digesta (Karasov and Martínez del Rio 2007). After early models of digestion were proposed (Penry and Jumars 1987), later work incorporated nutrient breakdown and absorption into the models to predict the ingestion rate that maximizes an animal’s net rate of nutrient absorption (for a review see McWhorter 2005).

Experimental and theoretical studies of animal foraging behaviour and energy assimilation demonstrate the interplay between the behavioural regulation of food intake and digestive efficiency (Martínez del Rio and Karasov 1990). My research focuses on the interaction between compensatory feeding and physiological constraints in nectarivorous birds exposed to energetically challenging conditions. I investigated whether these birds can match energy intake to their energy expenditure when experiencing variations in food quality and availability and metabolic requirements. In the following sections, I will introduce nectar as a food source and the avian nectarivores that consume it, before moving on to energetic challenges in these birds and the outline of my research.

Nectar as food source

Nectar is one of the most common foods, produced by plants as a reward for pollinators or defenders against herbivores (Nicolson 2007a). Nectar consumers come from a wide taxonomic range. A wide variety of insects feeds on nectar, including beetles (Coleoptera), true flies (Diptera), butterflies and moths (Lepidoptera) and bees, wasps and ants (Hymenoptera) (Nicolson 2007a). Vertebrate nectarivores embrace various bird and bat species (Nicolson and Fleming 2003a; Nicolson 2007a). Many non-flying mammals, including rodents, marsupials and primates, also visit flowers to feed on nectar, and play a role in plant pollination (Wiens et al. 1983; Carthew and Goldingay 1997). Lizards have also been identified as common nectar consumers, especially on islands (Olesen and Valido 2003). In addition, birds and mammals that are specialized on other diets also feed on nectar occasionally (Garber 1988; Symes et al. 2008). Not all nectar consumers benefit the plants: unwanted visitors include nectar thieves, which are morphologically unsuited to pollinate flowers, and nectar robbers, which puncture the base of flowers to access nectar (Nicolson 2007a).

What makes floral nectar such a desirable food source? Nectar is an easily digested food and rich in energy. It contains sugars predominantly in the form of the disaccharide sucrose or the monosaccharides glucose and fructose (Nicolson and Fleming 2003a). Nectar may also contain other sugars, such as xylose, which remains puzzling because pollinators are averse to this sugar (Jackson and Nicolson 2002). Besides sugar and water as major components, nectar further contains inorganic ions, enzymes, amino acids and lipids (Nicolson and Fleming 2003a; Nicolson 2007b; Nicolson and Thornburg 2007). Secondary compounds found in nectar, such as phenolics, alkaloids and terpenoids, may be toxic or repellent to some nectar consumers, while they attract others (Nicolson and Thornburg 2007).

Nectar sugars are synthesized in the nectary of flowers or derive from sucrose transported in the phloem sap (Nicolson and Thornburg 2007). The enzyme invertase, which is found in the nectary, hydrolyzes sucrose to its components glucose and fructose, thus determining the relative amount of each main nectar sugar (Pate et al. 1985). A dichotomy between sucrose and hexose nectars is evident in bird-pollinated plant species. In a large data set of 112 plant species in Costa Rica, sucrose was found to be the dominant nectar sugar in plants pollinated by hummingbirds (Stiles and Freeman 1993). The literature review by Nicolson and Fleming (2003a) supports this finding, as sucrose was the dominant nectar sugar found in most of the 278 hummingbird-pollinated plant species investigated in America. Plants pollinated by sunbirds and honeyeaters, on the other hand, showed a bimodal pattern, with about half of the nectars being hexose-dominant, whereas sucrose is the dominant sugar in the other half (Nicolson and Fleming 2003a). This dichotomy is not seen as a consequence of bird physiology, as specialist nectarivorous birds assimilate both sucrose and hexose sugars equally well (Lotz and Nicolson 1996). However, some occasional avian nectarivores lack the enzyme sucrase and can not hydrolyze sucrose, which appears to lead to aversion of sucrose nectars (Fleming et al. 2008).

Plants that are pollinated by birds or mammals produce large volumes of dilute nectar, compared to the smaller volumes of concentrated nectar of insect-pollinated plants (Pyke and Waser 1981; Nicolson and Thornburg 2007). In bird-pollinated flowers, the concentration of nectar ranges mainly from 15–30% w/w sugar (Nicolson and Fleming 2003a; Johnson and Nicolson 2008). However, nectar sugar concentration varies greatly both within and between food plants (Pyke and Waser 1981; Stiles and Freeman 1993; Nicolson and Thornburg 2007). Nectar of southern African passerine-pollinated flowers, for instance, ranges from 6.5% w/w (*Aloe speciosa*) to 36.7% (*Liparia splendens*) (Nicolson 2002). Nectar viscosity increases exponentially with concentration, which may affect the extraction of nectar from flowers (Nicolson and Thornburg 2007). Tongue licking frequencies and tongue loads of hummingbirds are influenced by high viscosities of the food source (Hainsworth 1973; Roberts 1995). A biophysical model of hummingbird feeding predicted optimal licking behaviour at nectar concentrations of 20–25% (Kingsolver and Daniel 1983).

Nectarivorous birds

Nectarivory has evolved independently in three major radiations of birds: sunbirds (Nectariniidae) in Africa and Asia, honeyeaters (Meliphagidae) in Australasia, and hummingbirds (Trochilidae) of the Americas. These avian nectarivores show morphological and physiological adaptations to their nectar-feeding lifestyle, such as brightly coloured plumages (Johnsgard 1983; Longmore 1991; Hockey et al. 2005), long straight or curved bills (Temeles and Kress 2003), specialized tongues (Hainsworth 1973; Schlamowitz et al. 1976; Downs 2004) and a gut adapted to nectar digestion (Richardson and Wooller 1986; Mbatha et al. 2002). Sunbirds, honeyeaters and hummingbirds are equally efficient in sugar uptake, assimilating between 95 and almost 100% of ingested sugar (Lotz and Schondube 2006). However, the ingestion of copious amounts of characteristically dilute nectar results in high energy costs for food warming (Lotz et al. 2003). Nectarivorous birds are also challenged by the elimination of excess water, and chronic diuresis is an inevitable consequence of their dilute food (Martínez del Rio et al. 2001; Nicolson 2007a).

Avian nectarivores have remarkably low nitrogen requirements, much lower than predicted by their body mass (Paton 1982; Roxburgh and Pinshow 2000; McWhorter et al. 2003). Their rates of endogenous protein turnover and loss of nitrogen in excreta are low (see McWhorter et al. 2003 for a review). It has been suggested that this is an evolutionary adaptation to their diet, which is low in protein (Tsahar et al. 2005). The amino acid content of floral nectar, although sometimes high (Nicolson 2007b), is insufficient to meet the nitrogen needs of nectarivorous birds; they rely on additional protein sources, such as pollen and arthropods (Paton 1982; Roxburgh and Pinshow 2000; Van Tets and Nicolson 2000). Their simple gut structure, adapted to the nectar diet, appears to make avian nectarivores less efficient at extracting protein than insectivorous birds (Roxburgh and Pinshow 2002): although the transit time of insects is longer in sunbirds than in similar-sized insectivores, only 60% of nitrogen is extracted by the sunbirds.

Nectarivorous birds are generally smaller than non-nectarivorous birds, with the family Trochilidae being the smallest sized birds in the world (Pyke 1980). Hummingbirds weigh 2–20 g, sunbirds 5–22 g and honeyeaters, being the largest of the nectar-feeding birds, weigh 8–250 g (Nicolson and Fleming 2003a). The small size of avian nectarivores is often associated with predicted low capacities for energy storage (e.g. Brown et al. 1978; Nicolson and Fleming 2003a). However, small hummingbirds may store considerable amounts of fat to provide energy for migration (Hiebert 1993). At the same time, fat storage implies higher flight costs, while a lower body mass reduces energy requirements (Calder et al. 1990; Chai et al. 1999). Small body size further entails energetic lifestyles and high mass-specific metabolic rates (Nicolson and Fleming 2003a). The energy balance of avian nectarivores is therefore likely to be affected by adverse environmental conditions, which makes them ideal subjects for investigating responses to energy stress.

Energetic challenges in avian nectarivores

Avian nectarivores have to feed frequently to meet their high energy requirements. Actively feeding hummingbirds use recently ingested sugars to fuel up to 95% of their metabolism, thus using essentially no stored fat (Carleton et al. 2006; Welch and Suarez 2007). Under energetically mild conditions and with food available *ad libitum*, nectarivorous birds accumulate energy steadily throughout the day (Wolf and Hainsworth 1977; Collins and Morellini 1979; Collins et al. 1980; Köhler et al. 2006). This energy accumulation over the entire day is necessary to sustain the birds at night when they do not feed (Fleming et al. 2004a; Köhler et al. 2006).

The energy balance of nectarivorous birds is strongly influenced by environmental factors. Firstly, wild birds encounter nectar of varying sugar concentrations while foraging on different food plants (Nicolson and Fleming 2003a). In addition, nectar can be drastically diluted by rain and high humidity (Tadey and Aizen 2001; Aizen 2003; Nicolson and Thornburg 2007). Despite varying nectar concentrations, birds are able to maintain a constant energy intake by adjusting their volumetric intake, which is commonly known as compensatory feeding (Nicolson and Fleming 2003b; see Martínez del Rio et al. 2001 for a review). However, if the sugar concentration is too low, birds are not able to compensate, as shown for whitebellied sunbirds (*Cinnyris talatala*), which lose body mass on a 3.6% w/w sucrose diet (Nicolson and Fleming 2003b). As nectar sugar concentration declines, sunbirds and hummingbirds increase the number of feeding events, while a nearly constant feeding event length is maintained (Wolf and Hainsworth 1977; Köhler et al. 2006). To my knowledge, only one study to date has investigated how quickly the feeding pattern is adjusted after changes in nectar concentration (Gass 1978): rufous hummingbirds (*Selasphorus rufus*) responded to an increased concentration within 10 min, primarily via adjusting their meal frequency, while their response to decreased concentration was preceded by a lag.

A second energetically stressful condition is the interruption of food intake, which birds may experience during migration, reproduction, unfavourable weather conditions and chases by predators or competitors (Glück 1987; Carpenter and Hixon 1988; Robin et al. 1988; Moore and Yong 1991). The loss of foraging time affects energy balance, especially of small birds, and can lead to depletion of energy stores. When the feeding of a wild rufous hummingbird was interrupted by a storm, it lost body mass but replenished its energy reserves within one day after feeding recommenced (Carpenter and Hixon 1988). Hummingbirds, exposed to fasting periods in the laboratory, were unable to increase their food intake after a fast to compensate for the loss in foraging time, and used torpor to compensate for the energy deficit (Hainsworth et al. 1981; Tooze and Gass 1985). Hainsworth et al. (1981) hypothesized that hummingbirds regulate feeding to maintain rates of energy accumulation which are set at dawn each day, and that the accumulated energy is not monitored during the day. Whitebellied sunbirds, on the other hand, were able to increase their rate of food intake following a fast (Nicolson et al. 2005).

Low ambient temperature is a third energetic challenge because it increases the costs of temperature regulation. Birds are expected to increase their dietary intake at low ambient temperatures in order to meet higher energetic requirements. Earlier studies suggest inter-specific differences in the ability of nectarivorous birds to compensate for low dietary energy content and high energy demands. Southern double-collared sunbirds (*Cinnyris chalybeus*), kept at 10–30˚C for two days and fed 0.4 or 1.2 M sucrose diets, increased their food intake in the cold and maintained energy balance on both diets (Lotz 1999). As examples for hummingbirds, Anna's hummingbirds (*Calypte anna*) nearly doubled their food intake over a 30˚C decrease in ambient temperature, whereas rufous hummingbirds showed only a slight increase in food intake (Beuchat et al. 1979; also see Beuchat et al. 1990 for a review). Different studies have revealed contradictory results for broadtailed hummingbirds (*Selasphorus platycercus*) that were rapidly exposed to 10˚C and fed dilute (0.25 and 0.29 M sucrose) and concentrated diets (1 M): in one study they did not increase their sugar intake and lost body mass (McWhorter and Martínez del Rio 2000), but in another they increased their intake and lost no more body mass in the cold than at moderate temperature (Fleming et al. 2004b).

Avian nectarivores may be able to maintain energy balance in the cold on concentrated diets, but their food intake may be restricted on low diet concentrations. When switched suddenly to low ambient temperature, rufous hummingbirds were able to meet their energy requirements on a relatively concentrated diet of 30% w/v sucrose, but not on lower concentrations (Gass et al. 1999). Whitebellied sunbirds, when exposed to 10˚C, increased their energy intake by 18% on a 1 M diet, but were not able to increase their intake on a very dilute diet of 0.1 M (Fleming et al. 2004b). These sunbirds were fed sucrose and equicaloric hexose solutions, and sugar type had an effect on their energy balance on a dilute diet (0.1 M) (Fleming et al. 2004b). Green-backed firecrowns (*Sephanoides sephanoides*), on the other hand, did not cope on any diet concentration at

15˚C, even after acclimation to the low temperature for seven days (Fernández et al. 2002).

These studies suggest that the food intake response of avian nectarivores under energetically stressful conditions is shaped by compensatory feeding and digestive constraint. When exposed to low sugar concentrations, low ambient temperature, or interruptions to feeding, birds compensate by increasing their intake. But when exposed to extremely low nectar concentrations, extremely low ambient temperature or extended losses in foraging time, birds may not be able to meet their energy demands because of physiological constraints to nectar ingestion and digestion, as well as osmoregulatory processes. Firstly, nectar ingestion may be limited by the rate at which nectar can be licked from flowers (Kingsolver and Daniel 1983). The amount of nectar that can be ingested may be restricted by the absence of a crop (Mbatha et al. 2002) or by stomach size (Bednekoff and Houston 1994). Ingesting large volumes of nectar is also energetically costly due to food warming costs (Lotz et al. 2003). Secondly, the digestive processing of nectar meals may be restricted by sucrose hydrolysis rates (McWhorter and Martínez del Rio 2000; Martínez del Rio et al. 2001) and the absorption of sugars (McWhorter et al. 2006; Napier et al. 2008). Thirdly, birds may face osmoregulatory problems when consuming large volumes, for example the disposal of excess water (McWhorter and Martínez del Rio 1999; Hartman Bakken and Sabat 2006) and loss of electrolytes (Fleming and Nicolson 2003).

Study species

My research focuses on avian nectarivores of the families Nectariniidae and Meliphagidae. I studied two sunbird species, namely the whitebellied sunbird, *Cinnyris* (*Nectarinia*) *talatala*, and the amethyst sunbird, *Chalcomitra* (*Nectarinia*) *amethystina*, and one honeyeater species, the brown honeyeater, *Lichmera indistincta*.

The whitebellied sunbird occurs widely in sub-Saharan Africa and is common in the north and north-east of South Africa (Cheke et al. 2001). It prefers semi-arid savannas and woodland, but can also be found in cities, particularly in gardens and parks (Hockey et al. 2005). It is resident or locally migrant and lives alone as well as in pairs or small groups (Hockey et al. 2005). Its average body mass is 7 g and the sexes are dimorphic in their plumage colouration, with males being brilliant iridescent green on the head and back, with a royal blue band on their chest, yellow pectoral tufts and an off-white belly; and females being greyish-olive (Skead 1967; Hockey et al. 2005). Whitebellied sunbirds forage on flowers of *Acacia*, *Eucalyptus*, *Strelitzia*, *Jacaranda*, *Protea*, *Leonotis* and other plants (Skead 1967).

The amethyst sunbird is endemic to central and sub-Saharan Africa (Cheke et al. 2001). In South Africa, it occurs in the northern region and along the whole east and south coast, preferring open woodland or bush, hillsides with *Aloe* species and suburban gardens and parks (Hockey et al. 2005). It is sedentary or locally migratory and lives alone, in pairs or groups (Cheke et al. 2001). The body mass averages 15 g and the sexes are dimorphic; males being black with an iridescent reddish-purple throat and a malachite green forehead, and females being brown with an off-white, streaked brown belly and blackish throat (Skead 1967; Hockey et al. 2005). Both whitebellied and amethyst sunbirds are characterized by a long, slender and curved bill (Downs 2004; Hockey et al. 2005). Food plants of amethyst sunbirds are species of *Strelitzia*, *Aloe*, *Protea*, *Erythrina* and *Eucalyptus*, among others (Skead 1967).

The brown honeyeater occurs in eastern, western and northern Australia and throughout New Guinea (Longmore 1991). It can be found in semi-arid shrub lands, forests and woodlands, as well as in suburban parks and gardens. This honeyeater species is locally resident and lives alone, in pairs or in small groups (Longmore 1991). The brown honeyeater is one of the smallest honeyeater species, weighing on average 10 g (Richardson and Wooller 1986). This species was chosen for my experiments as it is of comparable size to whitebellied and amethyst sunbirds. Male and female brown honeyeaters are both of dull olive-brown colour with a lighter belly and a characteristic small wedge-shaped patch of yellow or white behind the eye (Longmore 1991). Their bill is shorter than that of sunbirds and only slightly curved. Examples of food plants of brown honeyeaters include species of *Calothamnus*, *Eucalyptus*, *Grevillea*, *Hakea*, *Lysiana* and others (Hopper 1981).

Objectives of my research

My research focuses on the effects of nectar sugar concentration, fasting periods and ambient temperature on the feeding patterns, food intake and energy balance of sunbirds and honeyeaters. I aimed to compare the two main lineages of passerine nectar feeders with regards to their response to similar energetically challenging conditions.

In the first chapter of my thesis, I investigated whether the feeding duration of whitebellied sunbirds can provide an estimate of their meal size over a range of nectar sugar concentrations. This knowledge was essential for subsequent experiments, in which I needed to be able to use meal size as a surrogate for feeding duration of these birds. The custom-designed experimental equipment and software used in my study allowed for remarkably precise data collection. All feeding events of the bird were recorded with an infrared photodetection system, which was interfaced to a computer. In addition, nectar consumption and the body mass of the bird were recorded continuously (every 0.2 s) by electronic balances which were also interfaced to the computer. Food intake and body masses of whitebellied sunbirds have been recorded at hourly or daily intervals in previous studies (e.g. Nicolson et al. 2005), and my study is the first to provide information on a much finer scale. I predicted that meal size can be used as estimate of feeding duration on all diet concentrations.

Chapter 2 focuses on the response of whitebellied sunbirds to sudden changes in nectar concentration. My aim was to determine how rapidly these birds adjust their volumetric intake and feeding patterns after changes in diet concentration, when fed various sugar concentrations, ranging from 2.5–30% w/w sucrose, for 1.5 h each. Using the same experimental equipment as in Chapter 1, I continuously recorded feeding events and body mass in order to investigate whether the birds maintain a constant energy intake on various nectar concentrations and whether this is achieved by altering meal frequency and/or meal size. Nothing is known of how quickly sunbirds respond to a change in nectar concentration. I hypothesized that whitebellied sunbirds adjust their feeding frequency, and thus their food intake, within minutes after a switch in diet concentration.

In Chapter 3, the response of whitebellied sunbirds and brown honeyeaters to a fasting period during the photophase was investigated. I used a similar experimental design to those in previous studies (Tooze and Gass 1985; Nicolson et al. 2005) to allow for comparison. I predicted that, like whitebellied sunbirds (Nicolson et al. 2005), brown honeyeaters would adjust their food intake to compensate for the fasting period. However, in the case of the sunbirds, my aim was to collect data at a very fine temporal resolution to investigate the feeding patterns following the fasting period. I hypothesized that sunbirds increase their feeding frequency, rather than meal size, to adjust their food intake after the fasting period.

In another experiment, whitebellied sunbirds and amethyst sunbirds were exposed to low ambient temperature and varying nectar sugar concentrations (Chapter 4). Their food intake and body mass were recorded daily to determine whether the birds are able to adjust their food intake and maintain energy balance. I further recorded their feeding events using a photodetection system. As ambient temperature and nectar concentration decrease, birds were expected to increase the number of feeding events, rather than meal size. On moderate and concentrated diets, I predicted that the sunbirds would be able to increase their food intake sufficiently to maintain energy balance at low ambient temperature. When birds are fed dilute diets, however, I hypothesized that food intake might be limited by physiological constraints, leading to body mass loss.

In Chapter 5, brown honeyeaters were exposed to a similar temperature challenge. As in the case of sunbirds, I hypothesized that the honeyeaters would increase their food intake in the cold and maintain body mass on moderate and concentrated diets, but not on dilute diets. My experiment was conducted using both main sugar types in nectar (sucrose and hexoses). However, I did not expect differences in food intake and body mass between sucrose and hexose diets. My findings from the temperature challenge experiments were compared to the digestive capacities of brown honeyeaters as well as whitebellied and amethyst sunbirds predicted by a chemical reactor model, which assumes sucrose hydrolysis to be the limiting step in nectar digestion, and relies on knowledge of gut morphometrics, sucrase activity and sugar assimilation efficiency (McWhorter and Martínez del Rio 2000; Martínez del Rio et al. 2001).

The investigation of feeding patterns of sunbirds included the determination of feeding frequencies, feeding durations and meal sizes. However, one last aspect remains unidentified: tongue licking frequencies, durations of licks and food consumption per lick may change with changing viscosity, such as when nectar concentration (or ambient temperature) varies. Birds may also adjust these licking parameters after a fasting period, to maximize their food intake. My last thesis chapter (Chapter 6) describes the licking behaviour of whitebellied and amethyst sunbirds feeding on varying nectar concentrations with varying viscosities, and on days with and without a fasting period. No study to date has investigated licking frequencies and consumption per lick of avian nectarivores following a fast. My study is also the first to investigate licking behaviour in these two species. Early studies have recorded licking behaviour of avian nectarivores with video cameras (Hainsworth 1973; Collins et al. 1980), which may provide insufficient resolution. In my experiments, a photodetection system, providing remarkable fine-scale data recording (every 1 ms), was used to record tongue licks of the sunbirds. I hypothesized that licking frequencies and consumption per lick would decline, while lick duration would increase, with increasing sugar concentration due to increased viscosity of the solution. I further predicted that these licking parameters would not depend on the degree of starvation.

In summary, my research focuses on the behavioural and physiological responses of avian nectarivores to energetic challenges. I aimed to determine whether the response of sunbirds and honeyeaters to variations in nectar quality and availability, and ambient temperature, are shaped by compensatory feeding or physiological constraints. Furthermore, I investigated on a novel short-term scale how sunbirds adjust their feeding patterns in an attempt to compensate for alterations in energy intake or energy requirements.

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