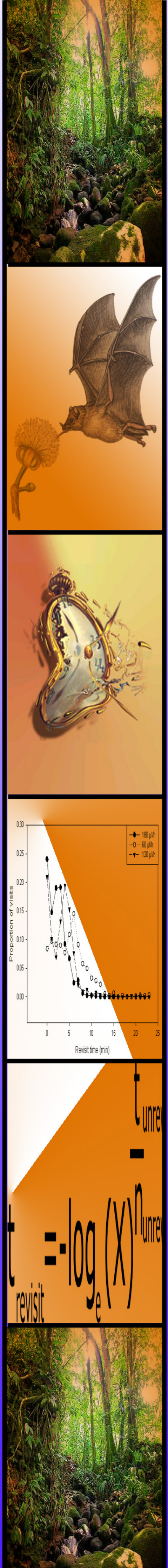
Bat Time Stories:

Decision-making in spatio-temporally predictable environments



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Time is the measurable unit of movement concerning a before and an after.

Aristotle

If you can look into the seeds of time,
And say which grain will grow and which will not,
Speak then to me.

Act I, Sc. III
Banquo in
'Macbeth' by
William
Shakespeare

There is surely no greater wisdom, than well to time the beginnings, and onsets, of things.

Francis Bacon

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Summary

SINCE ENVIRONMENTS UNDERLIE a constant change, animals need to keep track of these changes by gathering information and by using this information to make decisions. During the course of evolution, cognitive abilities, information processing skills, have evolved in many species to cope with the requirements of diverse habitats.

In this study I investigated the cognitive abilities involved in the foraging on renewable resources. Examples for such resources include nectar, fruits, or foliage. Renewable resources possess two qualities that can be used by an animal to optimise its foraging behaviour; first, once an animal discovers a location where such a resource can be found, it is profitable to return to this location later since most renewable resources are not mobile. Second, there is often a temporal pattern underlying the renewal process so that such a resource renews itself with a more or less constant production rate. Thus, it would be a clear advantage if an animal were able to remember the location and to estimate the production rate of a resource. To remember the location of a resource can save time and energy for searching, and the ability to assess the production rate would allow an animal to time its return so that the difference between the energy that is needed to travel to the resource and the energy gained at the resource is positive.

I explored these possibilities in a flower-visiting bat, *Glossophaga soricina*, which forages mainly on floral nectar. This species will thus allow for the study of cognitive specialisations in the domains of spatial memory and interval timing. This study aimed at the following questions:

1. What spatial information will these bats use to relocate already visited flowers and how is this information encoded?
2. Can bats use temporal and qualitative information that can be obtained when visiting a flower to time their revisits?
3. What implications arise from these results for the dynamics on a population level?

When relocating flowers, bats have several spatial stimuli available. However, some of these stimuli are spatially dissociated from the flower like conspicuous branches or leaves. When the spatial contiguity between a stimulus and a response location is not given, it is difficult or even impossible to form associations for some species. However, in the case of flower-visiting bats, it could be of advantage to use these stimuli in the relocation process. In chapter 2, I explored this possibility by providing the bats with additional cues in a task where they had to exploit an array of 64 flowers with 16 randomly distributed rewarding feeders. The additional cues were spatially separated from the rewarding feeders. Even though bats employed information from these spatially dissociated cues in the relocation process by forming single stimulus response location associations. However, the information obtained from additional cues seems, at least in this experiment, of subordinate importance since bats were even without cues able to achieve a good performance with respect to their spatial accuracy.

Bats encounter in their environments different species of flowers that provide them with nectar. The quality with respect to nectar content of these flowers can differ considerably between as well as within species. In chapter 3, I investigated, whether flower-visiting bats can discriminate between different sugar water volumes. This was done in a two alternative forced choice task in which two sugar water volumes were presented to the bats, which differed. Bats discriminated well between the different sugar water volumes. An analysis on basis of a psychometric function that we obtained from the empirical data showed that the discrimination threshold seems to be even lower than the threshold for honeybees.

The production rates of floral nectar underlie temporal patterns, and the ability to estimate the time interval since the last visit to a flower might help flower-visiting bats to time their revisits according to such patterns. In chapter 4, I examined, whether bats possess the ability to estimate small time intervals. For this purpose, I tested bats in a modified version of a fixed interval schedule, the peak procedure. Here, bats were rewarded after a fixed time after the onset of a signal. We analysed only empty trials, trials where no reward was given, that were interspersed with ordinary trials. Bats showed increasing response rates after the signal onset with maximum response rates at the fixed interval time. After the fixed interval time had elapsed, the response decreased again. This reaction has been already found in several other species. It shows that flower-visiting bats are able to estimate small time intervals, which might help them optimise their foraging bouts.

In the previous two chapters, I looked at the perception of nectar volumes and time intervals separately. However, only when bats were able to integrate these two information, it could result in an optimisation of their foraging behaviour. Therefore, I confronted bats with six feeders with differing nectar secretion rates (chapter 5). Results showed that bats adopted their visitation pattern according to the underlying rates. Moreover, a computational model could provide evidence that bats possess reference memories for the two types of information. Thus, bats are able to estimate

nectar production rates and direct their foraging decisions by this information.

In all paradigms described above, bats foraged alone. However, under natural conditions this is seldom the case. In chapter 6, I explored the possible ecological implications from chapter 2 through 5 and speculated on the impact of the found cognitive abilities on foraging dynamics on a population level. I tested several bats in the rainforest in Costa Rica in a semi natural paradigm for their reaction to variable resources while foraging in a group with other individuals. And even though the amount of empirical data is not convincing yet, I cannot rule out the possibility that the cognitive abilities we found might also constitute the basis for the estimation of competitional pressure at certain resource locations, which could lead to an optimised exploitation of the standing crop.

In this study I could provide evidence for the existence of several high level cognitive abilities in a flower-visiting bat. Through these cognitive abilities, bats can plan into the future and direct their foraging decision by the information they processed. It is probable that these cognitive abilities represent unique adaptations to the demands of the ecological niche of a flower-visiting bat.

Chapter 1

General introduction

Cognition and Evolution

ANIMALS POPULATE ENVIRONMENTS from deep sea to highest mountains and each species shows specialised adaptations to cope with their environment that have evolved during the course of evolution. Apparent adaptations include prominent morphological features like the lungs of tetrapod vertebrates for breathing outside the water, sharp teeth that enable carnivores to efficiently trench up their prey, or birds' wings. But besides the more or less visible morphological adaptations, cognitive abilities were shaped by evolution to meet the challenges of diverse environments. Cognition here is defined as 'the neuronal processes concerned with the acquisition, retention, and use of information' (Dukas 2004). However, neurological processes are hidden deep within an animal and are hard to observe directly. It is although possible to study the output of these neurological processes by observing the behaviour of an animal. By integrating the behavioural reaction of an animal and neurological data, one can receive deeper insights into the mechanism behind the behaviour.

Food hoarding birds, for example, with enhanced spatial memory show an increased hippocampus size compared to their non hoarding relatives (Healy & Krebs 1996, Krebs et al. 1996, Basil et al. 1996, Brodbeck 1994, Healy & Hurly 2004); birds that use tools to accomplish tasks that were naturally out of their morphological range show a proliferated neostriatum (Lefebvre et al. 2002) and the song repertoire of some birds, which is highly fitness relevant (DeVoogd 1998), is correlated with the volume of the song control nucleus high vocal centre (DeVoogd et al. 1993, Szekely et al. 1996).

Cognitive abilities, amongst others, enable animals to react to changes in their environment and thus to exhibit a behavioural plasticity that can cope with a broad spectrum of situations. However, complicated behavioural programs or cognitive traits incur a cost upon the animal as their basis consists of neurological material that is costly to build up and to maintain (Laughlin 1998). Thus, there is a trade-off between the amount of information that has to be processed and how valuable this information in terms of energy or ultimately fitness is for the animal (Laughlin 2004). Here, rules of thumb or heuristics represent an alternative, cost reduced solution when forced to come to a decision (Iwasa et al. 1981, Todd & Gigerenzer 2001). By using only a small but crucial part of the available information, animals can solve the problem of reacting adequately in the environment and at the same time saving costs for the neurological architecture. Often, applying heuristics can result in energetically nearly equivalent solutions that are 'fast and frugal' (Todd & Gigerenzer 2000). These solutions are often regarded as suboptimal from an omniscient point of view, but at a closer look prove to solve the trade-off between the cost for the processing of information and the gain from the decision-making process.

Foraging on floral nectar

In this thesis I investigated the cognitive abilities and decision-making processes involved in the foraging behaviour of nectar-feeding animals. Nectar-feeding animals can be found throughout the whole animal kingdom from invertebrates like ants, bees, and bumblebees to higher vertebrates like hummingbirds, bats, rodents, and even a gecko on New Zealand. These animals feed on the nectar, a sugar water solution, of flowers and, in the majority of cases, pollinate the flowers in return in one of the best known examples for mutualism. The co-evolution of flowering plants and their pollinators has produced a wide variety of life forms.

From an animals point of view the pollination aspect in this mutualistic relationship is rather unimportant, apart from pollen as a nutritional supplement. Important for a visit at flower is the nectar content, and this nectar content is to a certain degree predictable. First, flowers are non mobile and thus stable in respect to their location in space. This makes it possible to return to especially profitable flowers. Social bees, for example, signal, once they found a profitable flower, the direction and distance of this resource to the other bees in the hive via a complicated movement pattern, which encodes the position of the resource. Hummingbirds can remember which flowers they visited most recently (Henderson et al. 2001). This leads to the second characteristic of flowers. A lot of plants continuously reproduce nectar that has been removed so that the flowers will refill over time. This will make it profitable for a forager to return to such a flower, albeit not immediately, but at a later point in time. This led to the development of a so-called win-shift strategy in hummingbirds (Burke 2001). Here, hummingbirds rather fly to flowers that have not been visited yet than to return to an already visited flower. However, since the plants secrets nectar, it will become profitable to visit individual, already visited flowers again. Here, the question arises, when this point in time is reached and how animals can estimate it. What information will influence their decision to return? What strategies will be employed by an animal to solve the task of not returning too early to a particular flower, when the cost for getting to the resource is higher than the gain from it?

Experimental subjects

Throughout this thesis I concentrated on the cognitive abilities involved in the foraging behaviour of Pallas' long-tongued bat, *Glossophaga soricina* (Pallas), which lives in the Neotropis and shows specialised morphological and physiological adaptations to it's flower-visiting ecology (Winter & von Helversen 2001). The diet of this species does not exclusively include nectar, but also fruits, pollen, and insects depending on habit (Gardner 1977). Although not an obligate nectarivore, *G. soricina* feeds primarily on nectar in the Costa Rican rainforest during the dry season (Webster 1993). Animals weigh around 10 g with a wingspan of 20 cm to 25 cm.

These animals have one of the highest daily energy requirements ever measured in a eutherian mamal (Winter & von Helversen 2001). This makes them ideal objects for the study of foraging behaviour since they need to feed during the whole night and cannot stop for long because their reserves are limited.

A lot of Tropical plant species have specialised on the pollination of bats and show a special chiropterophile syndrome. These adaptations include specialisations in odour, shape, and colour that make it easier for nectar-feeding bats to find these flowers. When visiting a flower, *G. soricina* will change its flight pattern from ordinary flapping flight to a energetically more costly hovering flight in front of the flower (Winter 1998). The bat will then stick its head into the corona opening and lick with its extraordinary long tongue (Winter & von Helversen 2003) the nectar from the bottom of the flower.

Aim of this study

In the following, I will outline a typical foraging situation for *G. soricina* and describe what cognitive abilities I investigated that constitute important components for a flower-visiting bat to solve the task of foraging on a renewable resource.

At the beginning of a night, a bat will leave its roost and might have some prior knowledge where profitable sites can be found and will thus search there for food. Once it discovers a flower where nectar can be obtained, a bat should remember the exact location to return to it later. Here, two problems arise. How can a bat relocate this particular flower and when should it return?

To relocate flowers *G. soricina* could be shown to remember several distinct places and find back to them (Winter & Stich 2005). However, the shape, colour, or echo-acoustic structure of a flower could be misleading when several flowers of the same species, as happens frequently, are aggregated on a small scale. Here, cues that are not directly at a flower could help bats relocate a particular flower. Chapter 2 deals with the question whether and how bats use cues that are spatially dissociated from a goal, a flower, to find it.

However, even when finding back to a profitable flower, there is no guarantee that a bat can find nectar. The plant has to reproduce nectar after being emptied and only when the flower has refilled a bat should return to this flower. However, there are also costs associated with each visit at a flower. First, a bat has to fly to the location of the flower and second, *G. soricina* performs a hovering flight in front of the inflorescence in order to lick the nectar from the flower (Dobat & Peikert-Holle1985, Winter & von Helversen 2003). This hovering is, compared to normal flight, very costly (Winter 1998). Thus, bats should only return to a flower when enough nectar has been produced by the plant to compensate for the energetic costs of obtaining it. To estimate the point in time when a return to a flower is profitable, a bat has to assess the rate with which a plant produces nectar. The rate can be estimated by the bat when integrating two types of information; first, the amount of nectar received at a visit and second, the time interval that has elapsed since the last visit. To investigate whether bats are able to assess these two parameters at a flower, I tested if bats can discriminate between differing sugar water volumes (chapter 3) and explored the bats' ability to estimate small time intervals (chapter 4).

However, the important prerequisite to assess a production rate at a flower is to integrate the two informations about elapsed time interval and sugar water amount to time revisits. I tested this in chapter 5 and compared the empirical data to several computational models. Within these models, I explored several hypotheses of how the available information is employed by the bats. I was especially interested, what types of memory are involved in revisit decisions and if heuristics are applied for revisit decisions.

However, all earlier thoughts are based on the assumption that individuals live alone in their environments. But in natural environments intra- and interspecific competition is common. In chapter 6, I explored possible implications from chapter 2 through 6 for foraging dynamics on a population level. How can bats use the information they receive from a visit at a flower to estimate competitional pressures. Moreover, are bats able to react to changes in resource availability that are caused by competition? Within this chapter, I developed a new theory of how bats might be able to use the information about the variability in amount at certain resource locations to their advantage so that a population of bats will exploit the standing crop of available nectar in an efficient way.

Literature

Basil, J. A., Kamil, A. C., Balda, R. P., and Fite, K. V. (1996). Differences in hippocampal volume among food storing corvids. *Brain Behavior and Evolution, 47,* 156-164.

Brodbeck, D. R. (1994). Memory for Spatial and Local Cues - A Comparison of A Storing and A Nonstoring Species. *Animal Learning & Behavior, 22,* 119-133.

Burke, D., Cieplucha, C., Cass, J., Russell, F., and Fry, G. (2002). Win-shift and win-stay learning in the short-beaked echidna (Tachyglossus aculeatus). *Animal Cognition, 5,* 79-84.

DeVoogd, T. J. (1998). Causes of avian song: using neurobiology to integrate proximate and ultimate levels of analysis. 337-380.

DeVoogd, T. J., Krebs, J. R., Healy, S. D., and Purvis, A. (1993). Relations Between Song Repertoire Size and the Volume of Brain Nuclei Related to Song - Comparative Evolutionary Analyses Amongst Oscine Birds. *Proceedings of the Royal Society of London Series B-Biological Sciences, 254,* 75-82.

Dobat, K. and Peikert-Holle, T. (1985). Blüten und Fledermäuse (Chiropterophilie). Frankfurt: Kramer Verlag.

Dukas, R. (2004). Evolutionary biology of animal cognition. *Annual Review of Ecology Evolution and Systematics, 35,* 347-374.

Gardner, A. L. (1977). Feeding Habits. 293-350.

Healy, S. D. and Hurly, T. A. (2004). Spatial learning and memory in birds. *Brain Behavior and Evolution, 63,* 211-220.

Healy, S. D. and Krebs, J. R. (1996). Food storing and the hippocampus in Paridae. *Brain Behavior and Evolution, 47,* 195-199.

Henderson, J., Hurly, T. A., and Healy, S. D. (2001). Rufous hummingbirds' memory for flower location. *Animal Behaviour, 61,* 981-986.

Iwasa, Y., Higashi, M., and Yamamura, N. (1981). Prey Distribution As A Factor Determining the Choice of Optimal Foraging Strategy. *American Naturalist, 117,* 710-723.

Krebs, J. R., Clayton, N. S., Healy, S. D., Cristol, D. A., Patel, S. N., and Jolliffe, A. R. (1996). The ecology of the avian brain: Food-storing memory and the hippocampus. *Ibis, 138,* 34-46.

Laughlin, K. and Mendl, M. (2004). Costs of acquiring and forgetting information affect spatial memory and its susceptibility to interference. *Animal Behaviour, 68,* 97-103.

Laughlin, S. B., van Steveninck, R. R. D., and Anderson, J. C. (1998). The metabolic cost of neural information. *Nature Neuroscience, 1,* 36-41.

Lefebvre, L., Nicolakakis, N., and Boire, D. (2002). Tools and brains in birds. *Behaviour, 139,* 939-973.

Szekely, T., Catchpole, C. K., DeVoogd, A., Marchl, Z., and DeVoogd, T. J. (1996). Evolutionary changes in a song control area of the brain (HVC) are associated with evolutionary changes in song repertoire among European warblers (Sylviidae). *Proceedings of the Royal Society of London Series B-Biological Sciences, 263,* 607-610.

Todd, P. M. and Gigerenzer, G. (2000). Precis of Simple heuristics that make us smart. *Behavioral and Brain Sciences, 23,* 727-+.

Webster, W. D. (1993). Systematics and Evolution of Bats of the Genus Glossophaga soricina. Lubbock: Texas Tech University Press.

Winter, Y. (1998). Energetic cost of hovering flight in a nectar-feeding bat measured with fast-response respirometry. *Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology, 168,* 434-444.

Winter, Y. and Stich, K. P. (2005). Foraging in a complex naturalistic environment: capacity of spatial working memory in flower bats. *Journal of Experimental Biology, 208,* 539-548.

Winter, Y. and von Helversen, O. (2001). Bats as Pollinators: foraging energetics and floral adaptations. Pages 148-170 *in* L. Chittka and Thomson, J.D. eds. Cognitive ecology of pollination. Cambridge University Press, Cambridge.

Winter, Y. and von Helversen, O. (2003). Operational tongue length in phyllostomid nectar-feeding bats. *Journal of Mammalogy, 84,* 886-896.

Chapter 2

Density dependence of spatial cue facilitated foraging by a flower bat.

Abstract

It is crucial for nectar-feeding animals to relocate profitable flowers. However, neither flower shape nor colour provides a salient cue to determine the nectar content of a single flower, especially when multiple flowers of the same species are aggregated on a small scale. In this study we investigated the effect of local cues that were spatially separated from the goal (min. 40 cm distance) on the foraging behaviour of a nectar-feeding bat, *Glossophaga soricina*, in a multiple goal finding task. Results show that an increase in local spatial cues facilitates better accuracy in relocating rewarding feeders. This will help bats to identify profitable flowers on a small scale. This effect is mainly brought about by single cue goal associations and not by the use of geometric outlines of experimental cues.

Introduction

WHEN MOVING THROUGH space, animals often need to find their way back to places they have visited before. To do so, animals may be guided by idiothetic mechanisms (e.g. *Cataglyphis fortis*; Müller & Wehner 1988) or incorporate salient (allothetic) cues in their mental spatial representation to support their ability to orient themselves in space.

These cues can be divided into global cues and local spatial cues. Global cues can be seen from a large area and change their direction only marginally when an observer changes his position. On the contrary, local cues can be seen (or which ever sense might be applicable) from a small distance and move within the reference frame with respect to the movement of the animal (Steck & Mallot 2000).

When it comes to relocating an exact position in space, global cues can guide the animal to a general goal area but local cues are often used to refine the search and acquire higher accuracy (Jacobs & Schenk 2003, Cheng & Spetch 1998).

The simplest case of relocating a goal by cue use is when goal and cue are in the same position in space. In this case the cue acts as a beacon to guide an animal directly to the spot. As the distance between goal and beacon increases, the beacon will no longer serve as a direct cue but instead become a local cue. Local cues are spatially dissociated from the goal and their associative strength for predicting the goal location is decreased. Thus animals may prefer cues that are near to the goal (Bennett 1993). Local cues can be incorporated into the spatial representation of animals as cue-goal associations (Gould-Baierle & Kamil 1999) or as a geometrical configuration of local cues (Cheng 1986 , Benhamout & Poucet 1998, Jones et al. 2002, Vargas 2004).

However, the diminishing associative strength with increasing distance between goal and local cue will lead to an increased spatial error (Brown & Gass 1993, Brown 1994). Moreover, the establishment of an association can be prevented altogether by the increased distance (Iwai et al. 1986).

Flower-visiting animals face a special situation. On one hand, flowers provide the animals with conspicuous direct cues (‘nectar guides’) that lead animals like a beacon to the inflorescence. Evolution has shaped the appearance of many flowers to match the perceptional abilities of their main pollinators. Hummingbirds, for example, are lured especially to flowers that have red inflorescences. Nectar feeding bats use echo reflective, olfactory and visual cues to find flowers (von Helversen and von Helversen 1999, Winter et al. 2005, Winter and Stich unpubl. Data).

On the other hand, however, the floral signals given by the shape and colour of the plant can be misleading with regard to the nectar content. Often several flowers of the same species stand close together and look more or less alike, but the nectar content of such flowers can vary significantly (Pacini et al. 2003). The possibility of confusing two flowers with each other is rather high. Thus, flower colours, shapes, or odours might be strong salient cues to indicate flower location but these cues might have little value for distinguishing between profitable and empty flowers.

Consequently, nectarivores also use surrounding local cues that are dissociated in space from a flower to remember crucial locations. In hummingbirds the relocation of flowers is facilitated more by global cues or spatial arrangement of flowers, dependent on inter flower distance, than by colour cues (Healy and Hurly 1998, Hurly and Healy 2002).

In this study we investigated whether the availability of local cues influences an animal's ability to remember individual flower positions within an array of flowers that look alike. We were particularly interested in the effect of cue density on associative learning speed and accuracy scores. With an increasing number of cues, the average distance between cues and goals decreases and the potentially increasing salience of the local cues should lead to higher accuracy scores. However, at high cue densities each single cue might lose its salience. When too many similar cues are aggregated on a small scale the cues themselves could be confused with each other. Here, we expected a drop in performance and an increase in errors.

We tested the ability of a Neotropical flower-visiting bat, *Glossophaga soricina*, to memorise several rewarded feeders in a three dimensional foraging paradigm. This bat species shows specialised adaptations to the ecological niche of a nectar feeder. Like other nectarivores, *G. soricina* uses mainly spatial information to relocate rewarding feeders (Thiele and Winter 2005). And there are first evidences that Glossophagines can solve the problem of finding a non-visible goal by using the configuration of two visual landmarks (Winter et al. 2005).

We confronted bats with a semi-natural environment where they could freely forage and provided them with differing densities of experimental local spatial cues that were spatially separated from the goal. This study was aimed at the learning efficiency of an animal under semi-natural conditions where several goals and different types of information are available.

Materials and Methods

Animals

Seven bats of the species *Glossophaga soricina* (Phyllostomidae) bred in captivity were used for this study. The climatic conditions both in the animal keeping facility and in the experimental room were 22°C and approx. 60% rel. humidity. The diet consisted of 17% honey water to which Nektar Plus or Nutricomp were added in addition to dry pollen. Artificial nectar from experimental food dispensers was a 17% sugar solution made from sucrose, glucose and fructose in equal parts, as found in the nectar of bat-visited flowers (Baker et al. 1998). Before each nightly experiment, bats received 1 ml of honey water (i.e. about 8% of daily intake) and after nightly experiments food ad libitum. Light conditions were LD 12:12 and all experiments with the echo-locating bats were conducted during the scotophase.

Experimental apparatus

The experiment tested a single bat in a foraging paradigm with a spatial and a temporal component. Bats had to find and remember 16 rewarding feeders out of an array of 64 feeders. The treatment consisted of presenting a variable amount of echo acoustic stimuli that served as local spatial cues.

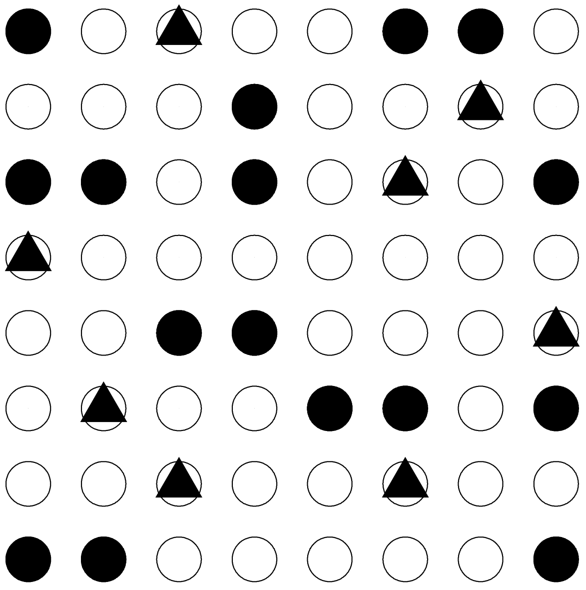

Figure 2.1: Sample distribution of 16 rewarding feeders (filled circles) and 8 landmarks (triangles) at the 64 feeder array.

The experimental testing apparatus was an array of 64 artificial nectar feeders (Winter and Stich 2005) with feeders arranged in an 8 by 8 rectangular configuration along the vertical plane with a distance of 0.4 m between each other (Figure 2.1). Feeders had a cylindrical PVC opening equipped with a photo-electric barrier to automatically detect visiting bats. For a reward, a valve at the backside of the array opened with an audible click and a syringe pump delivered an amount of 15 µl odourless sugar water to the base of the feeder opening, which bats removed by licking (Winter and von Helversen 2001).

Feeders were of identical appearance but each of the 64 feeders carried a one-sided echo acoustic stimulus (hollow sphere with holes) at a motorized swivel arm above it. Rotation of the swivel arm allowed us to make feeder positions distinct, by selectively displaying stimuli above specific feeders. Echoacoustic stimuli were acoustically inconspicuous if rotated to the back due to sound deadening material (noise-insulation board, PANA Schaumstoff GmbH, Geretsried) affixed to their back side.

Pre-Training

During experiments, two or three bats were kept individually in cages (0.7 m X 2.2 m X 1.5 m) placed within the experimental room. After moving from the animal keeping facility, bats were acclimated to their cages for one day with ad libitum food from a food bowl. On the second day bats were individually trained to learn to feed from the experimental array of feeders where the complete set of all 64 feeders was rewarding. Detection of feeders was facilitated by coating the the tips of the feeders with honey. Each bat easily learned to use the feeders, and was allowed approximately 400 visits to the array, which took about three hours, before it was returned to the cage and the next bat was released. Two to three bats were trained successively within a single night for most groups. To accustom the bats to the time component in the upcoming task, each active feeder was programmed to be inactive for a three-minute time interval after each rewarded visit. All bats visited at least 90% of the 64 different feeders during their 400 visits the first night.

Distribution of rewarding feeders and experimental spatial cues

During the individual experiments, only 16 out of the 64 pseudo-randomly distributed feeders gave nectar rewards. Distributions were determined by a pseudo-random procedure with the following rules: i. no three feeders in a row vertically or horizontally gave a reward; ii. no more than five rewarding feeders per quadrant of the array; iii. distributions with a seemingly regular pattern were excluded.

During the experiments a number of echo-reflective, local spatial cues were also presented within the feeder array. The number of such cues during the different experimental treatments was varied between 2, 4, 8 and 16. They were always placed above a feeder that did not give reward during an individual experiment and they were distributed regularly over the array. Positions were determined by first dividing the array in as many sub-areas as landmarks to be placed and then selecting a random position within each sub-area (for an example of the placement of 8 such cues see Figure 2.1).

Experimental procedure

During a single experiment a bat had to solve the task of obtaining food from 16 positions within the 64 feeder array. These positions were initially unknown to the bat due to the uniform outer appearance of both rewarding and non-rewarding feeders. The uniform array had an experimentally controlled component to its spatial structure. This was caused by a varying number of displayed echoacoustic stimuli serving as local, spatial cues. A single experimental night entailed 600 visits of a bat to the feeder array. Two times during this series of events, after 150 visits and after 350 visits, half of the landmarks were removed by automatically turning them to the back and thus behind their sound absorbing shield (for a duration of 50 visits). No appearance of the experimenter in the experimental room was necessary for this computer-controlled manipulation.

All bats received six different treatments, including controls. Treatments varied in the number of spatial cues presented. In the first night bats had no landmarks (control); in the next four nights each bat was confronted with 2, 4, 8 and 16 landmarks in randomised order. During their last experimental night, bats were given another control without any landmarks to test for an overall effect of learning. As in the training phase a feeder was in inactivated for three minutes after delivering a reward.

Data acquisition and statistics

The data collected for this study were the behavioural events of visiting a feeder recorded by computer. We determined the following parameters for each interval of 50 visits, for each animal and for each treatment:

a. Total number of visits (always 50).
b. Visits to potentially rewarding feeders, i.e. all visits to a feeder that could give nectar regardless of the actual reward status.
c. Number of rewards. The number of rewards collected by a bat.
d. Inter-visit interval: the time interval between two visits at the same rewarding feeder.

We used generalized linear models (R library geepack) to test for the potential effects of these factors on the experimental treatment. Factors initially included in the full model were:

a. Treatment: Number of cues coded as a factorial variable (0, 2 ,4, 8 and 16).
b. fifty_block: Each fifty visits equalled one block of fifty visits, e.g. fifty_block=3 are visits 101 to 150.

The full model consisted of these factors and their interactions;

Due to the repeated measures design, we used generalised linear models with general estimating equations (GEE). We assumed an autoregressive structure in the covariance matrix for the individual bats i.e. that visits of an individual are not independent of each other. The factors in the general estimating equations (GEE) were backwards eliminated using a $p<0.05$ criterion for the Wald Chi-square in the likelihood ratio until a minimum adequate model was found or no convergence of the data with the model could be detected. We assumed binomial distributions for proportional data and poisson distribution for count data as suggested by Crawley (2002). We used the built-in link functions provided by R. For the binomial and poisson data types, the median rather than the mean is given in the results.

Results

All seven bats could be trained to visit the feeders. They finished each nightly experiment (600 visits) within a time span of between two and four hours. In six out of 42 cases the experiment was terminated before 600 visits were made within four hours.

Visits to potentially rewarding feeders

As expected for a learning situation, all animals initially visited the 16 rewarding out of 64 total feeders at approximately chance level (0.28 SD ± 0.07) during each single experimental night and there was no significant deviation from the control level of the different treatments in a post-hoc test ($p>0.05$) (Figure 2.2). The number of correct visits (visits to potentially rewarding feeders) increased with the experience of the animals during a night. This was modelled by a positive ($B=0.04$) influence of number of visit on the visits to rewarding feeders (fifty_block: Wald $\chi^2=148.1$; DF=1; $P<0.01$). The increase in performance was also dependent upon the number of experimental landmarks (treatment x fifty_block: Wald $\chi^2=18.5$; DF=4; $P<0.05$). Thus, the rate of learning during a night was positively affected by availability of landmarks. A post-hoc test revealed that a significantly positive deviation from the control performance was only detected for 4 and 8 experimental landmark treatments (all p<0.05). Surprisingly, this effect did not extend to the 16 landmark condition. For the 16 landmark condition, the slope of the learning curve was no different from the control (p=0.34).

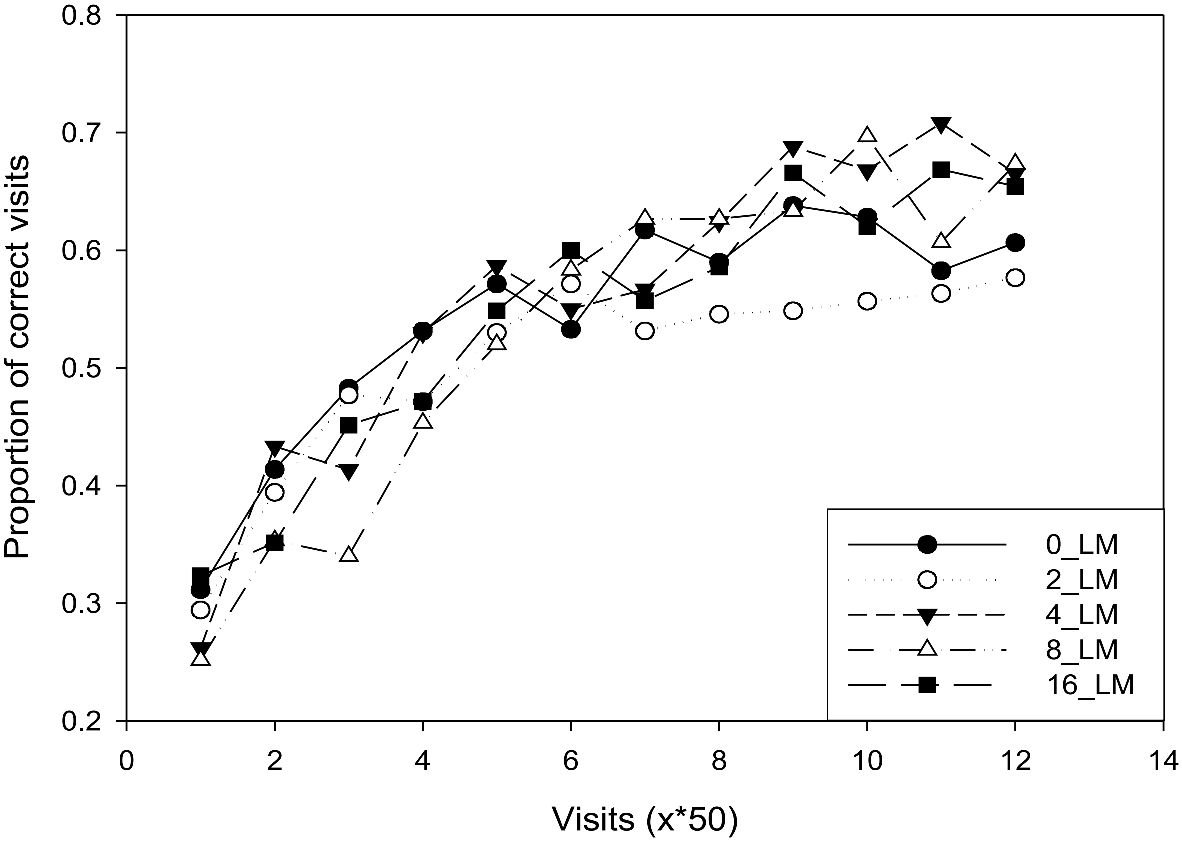

Figure 2.2: Proportion of visits directed at potentially rewarding feeders in the 64 feeder array. Data points are means for seven animals. Results for the two controls are shown as single curves. Abscissa gives visits in multiples of 50. Ordinate: Proportion of visits to rewarding feeders

Non-rewarding feeders with cues

Some of the non-rewarding feeders had (dependent upon treatment) echoacoustic cues serving as experimental landmarks placed directly above them (at a 2 cm distance). This raises the question if bats specifically avoided such marked, and never baited feeders. If bats avoided non-rewarding feeders with experimental cues then they should visit them less frequently than other non-rewarding feeders. We compared the visitation rate of such feeders to the average visitation rate of all non-rewarding feeders. This value was calculated from the number of total visits to non-rewarding feeders divided by 48 (the total number of non-rewarding feeders). Should the bats avoid feeders in the direct vicinity of the cues they should be visited significantly less often than average. Visits to expected and observed values at feeders near cues were significantly different from each other (one-sided Wilcoxon-Signed Rank Test; all $p<0.05$). Thus bats seemed to systematically avoid feeders in direct vicinity to cues.

This previous finding raises the question if the increased visitation of rewarding feeders simply resulted from avoidance of a specific subset of non-rewarding feeders. However, when excluding all feeders in direct vicinity to cues, the number of visits to potentially rewarding feeders in one experimental night was still much higher than expected by chance visitation alone (2 cues: 18.2 SD ± 2.9, expected: 9.1; 4 cues: 18.9 SD ± 1.6, expected: 8.8; 8 cues: 18.0 SD ± 4.2, expected: 9.1; 16 cues: 20.8 SD ± 2.9, expected: 10.8; Wilcoxon-Signed Rank Test; H0: expected – observed = 0; all $p<0.05$).

Number of memorized feeders

We analysed whether or not the number of feeders that an animal remembered was influenced by the different numbers of landmarks presented. For this we determined which and how many feeders were visited above chance level in order to arrive at an estimate of the number of memorized feeders for each treatment. Chance visitation assumes that all feeders had the same probability of visitation without knowledge of rewarding feeders. However, bats systematically avoided all feeders with cues (see above). Thus, we excluded all feeders in the direct vicinity to cues from the following analysis. A simple approach to calculating the rate of chance visitation is to divide the number of visits to potentially rewarding feeders by the number of all feeder visits, excluding feeders in the direct vicinity to cues. This measure will be appropriate when we look at a hypothetical bat that will visit infinite times. However, bats in this experiment visited feeders only 600 times and sometimes less. Thus, bats could well deviate from this measure and still visit the feeder at chance level. Therefore, we calculated the upper 95 % confidence limit of the probability that a bat would visit a certain feeder when visiting n times total with a number of available feeders equal to f. We used an approximation method to determine the confidence interval for the chance of visiting a certain feeder (Agresti and Coull 1998). The parameter n was calculated for each animal and each treatment by taking only the visits to feeders that were not in the direct vicinity to the cues. Parameter f was calculated by subtracting the number of cues from 64 (total number of feeders). We used the ‘approx.pois’ function of the epitools library in R (www.mathepi.com/epitools). For each animal and treatment we obtained an upper confidence limit for the animal's likelihood of visiting a certain feeder. We multiplied this probability by f to compute the necessary number of visits to a single feeder that would exceed chance visitation. Then we counted the visits to each potentially rewarding feeder for each treatment and animal and compared it to the expected value. All feeders with more visits than the expected value were considered memorised by the bat for the purpose of this comparative analysis (Table 2.1).

Table 2.1: Median number of remembered and found (at least visited once) potentially rewarding feeders for each treatment.

Treatment (no of cues)	***Median of found potentially rewarding feeders***	***Standard deviation of found potentially rewarding feeders***	***Median of remembered potentially rewarding feeders***	***Standard deviation of remembered potentially rewarding feeders***
0	15	3.01	6	2.47
2	13	1.13	5	1.63
4	15	1.38	5.5	1.87
8	15	1.00	6	1.00
16	14	1.27	7	1.46

However, the number of rewarding feeders that were found by a bat during each specific experiment could also influence the number of feeders that a bat remembered. That is, when a bat found only 6 of the 16 potentially rewarding feeders, this would automatically limit the number of remembered potentially rewarding feeders. Thus, we modelled a GLM (GEE) in which the dependent variable was the number of remembered rewarding feeders (assuming poisson errors). We included the logarithm of the number of found feeders as an offset parameter in the model. The logarithm was used because we used a log link function. The result of this analysis can be stated briefly. The treatment had no effect on the number of memorised feeders (Wald χ^2=5.96; DF=4; P=0.2).

Rewards

The proportion of visits to rewarding feeders is also an indicator for the spatial precision with which the animals were able to remember reinforced positions within the 64 feeder array. However, the experimental design demanded that bats not only remembered spatial locations but also avoided feeders after a reward for the fixed interval of three minutes. This task required spatial working memory. Here, we tested whether spatial cues had an impact on the working memory of the bats for their visits at the feeders. Thus in a first step we tested whether the number of rewards per potentially rewarded visit differed between treatments. In a second step we tested if such a possible change was facilitated by an enhanced working memory for recently visited feeders.

Bats increased the rewards per potentially rewarded visits with increasing cue densities (treatment: Wald χ^2=24.2; DF=4; P<0.05). This effect was independent of the course of the experiment (fifty_block: Wald χ^2=1.5; DF=4; P=0.21). The difference between cue treatments was very low, so we merged the factor levels of the treatment to only two factors (with or without cues) to see if there was a difference in explanatory power between the two models. This clearly was not the case (comparison of the two models: Wald χ^2=0.42; DF=3; P=0.93), thus there seemed to be a general positive effect of the cues upon the number of rewards collected by bats that did not differ between the cue treatments.

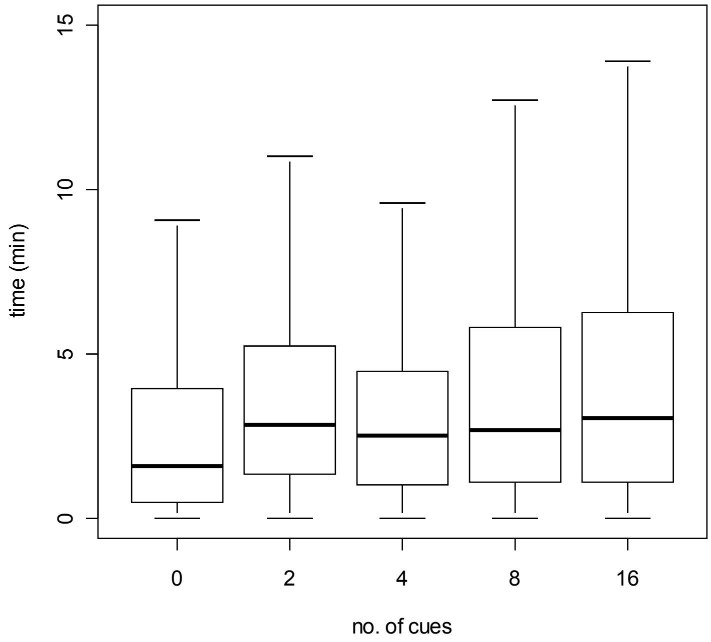

Figure 2.3: Boxplots of revisit times at potentially rewarding feeders for each treatment. Outliers are omitted.

Bats could increase the ratio of rewards / visit at a rewarding feeder either by an overall reduction of visits or by specifically not visiting during the three minute inactive period of a feeder. The increase in the reward ratio with the presence of landmarks might have been due to an adaptation to the underlying temporal pattern in the cued treatments, namely that bats will wait longer before revisiting a particular feeder. We tested this by assuming that the time interval before a revisit occurred could depend upon the number of cues. The revisit time intervals to a feeder could also depend upon the course of the experimental night. In the following we modelled a GLM (with GEE) with the time interval until a revisit occurred at a particular feeder in dependence of the treatment and the course of the experiment (assuming a gamma distribution for time intervals with an inverse link function).

The presence of cues facilitated an avoidance of rewarding feeders, resulting in bats making longer breaks between visits to a particular feeder (treatment x fifty_block: Wald χ^2=23.15; DF=4; P<0.01) (Figure 2.3).

Half cues hidden from bats

At two points during the experiment half of the cues were turned behind a sound absorbing material so that the right half of the array was free from cues. We compared the number of visits to a rewarding feeder during the turned back period to the average of the fifty visits before and after this period in the 4 and 8 cue treatment. There were no significant differences between the number of visits to rewarding feeders to the right side before and after the turning of the cues in either treatment (4 cues turn: Wald χ^2=0.02; DF=1; P=0.89; 8 cues turn: Wald χ^2=0.08; DF=1; P=0.78).

Discussion

In this study we investigated the effects of local spatial cues on the foraging efficiency of a nectar feeding bat, *Glossophaga soricina.*

Bats demonstrated their ability to memorise at least part of a novel distribution of sixteen rewarding feeders during a short time interval (2 to 4 hours). They learned to seek rewarding feeders and to avoid non-rewarding feeders. Even in the control, bats achieved high accuracy scores for the relocation of rewarding feeders, approximately 60 % which is far above 25 % for random choice. However, the performance was even further increased in the presence of four and eight experimental cues, which were spatially dissociated from the goal. The observed increase was not caused by an avoidance of feeders in the direct vicinity to cues, which were always unrewarded. If an avoidance of feeders in the direct vicinity to the cues would account for the differences found in accuracy, the effect should have been strongest with 16 cues. However, the performance in the 16 cue treatment was not significantly different from the performance of the control. Moreover, visitation to rewarded feeders did not drop to chance level when excluding feeders in the vicinity of the cues from analysis. Also, the total number of remembered feeders did not differ between treatments so that high performance values could not be obtained by constantly visiting only a single feeder. Thus, the presence of additional experimental cues facilitated a more accurate reference memory for the location of a goal. This effect was, as in hummingbirds (Brown and Gass 1993), present even though the cues were spatially separated from the goal. This underlines the special need of nectar feeding animals for local cues that help discriminate between single flowers in a small area.

However, with regard to the good performance in the control and the relatively small increase though the presence of cues, this mechanism seems to be only part of other processes neccessary to establish a spatial memory that will help to relocate resource locations. This is further supported by the fact that there was no detectable effect resulting from the turning of the cues. Here, other spatial cues or idiothetic mechanisms were used by bats to relocate feeders that gave a reward. This prevented a decline in performance during the phase when the experimental cues were turned to the back.

The constant performance during the turning of the cues also showed that there was no overshadowing effect by single cues as Gould-Baierle and Kamil (1999) could detect in their study with Clark's Nutcrackers. This effect would occur when the salience of a cue for a goal location is very high such that no other spatial information is included in the mental spatial representation to relocate the goal. Thus, the experimental cues had only medium to low salience for predicting a goal location.

Interestingly, the treatment with 16 experimental cues had no effect beyond avoidance of feeders with cues in the direct vicinity. So why did the experimental cues in the 16 cue treatment constitute no reliable cue for relocation? All experimental cues looked alike which could result in a confusion effect. Bats that make mistakes or 'feel unsure' whether the feeder they visited recently was a potentially rewarding one, when no reward is given, may reorient with the help of a known nearby cue. In the 16 cue treatment there are several nearby cues and thus confusion between cues that look alike is possible. For example, a bat visits a feeder and receives no reward. It visited this feeder before and now needs to cross check whether this is the correct feeder. If this feeder were the correct feeder, the bat would expect a cue directly to the right. Due to the regular lay out of the cues in relation the goal area, the combination between cue and distance and vector to a rewarding feeder could occur more often. Thus the salience for a single cue is reduced drastically such that no or only small informational value is imparted by a cue. In all likelihood, it was not possible for bats to perceive the whole array in the experiment. In the total darkness of the experimental room bats can rely only on their echo acoustic sense with limited radius and range. Thus a formation of single cue response location associations seems more likely than an orientation by the geometric outline of the cues. This view is supported by findings for *G. soricina* at a touch screen where a bat oriented visually and had two cues to relocate a hidden goal. Here, the bat also chose only one cue for orientation and then found the goal by using a vector and a distance from the cue (Winter et al. 2005). Bats do not seem to use a geometric outline of cues to relocate a goal.

The results further suggest that the presence of cues enhances the working memory for recently visited feeder so that bats are able to significantly reduce their revisit time intervals at a rewarding feeder. Before the experiment started, bats had already experienced the three minute period of inactivation following a reward. The revisit time interval in the control relates to the revisit time intervals of both experimental control nights. As a reminder, there was one experimental control night before and one control night after the experimental nights when additional cues were presented. It is thus unlikely that this enhanced working memory effect could be caused by the progression of the experiment. At this point the authors can find no plausible reason for this phenomenon and comments are most welcome.

To summarise, bats were able to learn to use cues that were spatially separated from the goal as direct predictors for rewarding feeders. There is evidence that bats used direct cue goal associations to relocate particular feeders. And even though there is no direct spatial contiguity between conditioned stimulus and the reinforcer, bats are able to form spatial associations. This ability of nectar feeding animals seems to be an adaptation to the problem that cues that are near the goal, such as flower petals, corolla, prominent leaves, provide no salient cue for the reward status of a particular flower and that bats often have to distinguish on a small scale between flowers that all look alike.

Literature

Agresti, A. and Coull, B. A. (1998). Approximate is better than "exact" for interval estimation of binomial proportions. *American Statistician, 52,* 119-126.

Baker, H. G., Baker, I., and Hodges, S. A. (1998). Sugar composition of nectars and fruits consumed by birds and bats in the tropics and subtropics. *Biotropica, 30,* 559-586.

Benhamou, S. and Poucet, B. (1998). Landmark use by navigating rats (Rattus norvegicus): Contrasting geometric and featural information. *Journal of Comparative Psychology, 112,* 317-322.

Bennett, A. T. D. (1993). Spatial Memory in A Food Storing Corvid .1. Near Tall Landmarks Are Primarily Used. *Journal of Comparative Physiology A-Sensory Neural and Behavioral Physiology, 173,* 193-207.

Brown, G. S. (1994). Spatial Association Learning by Rufous Hummingbirds (Selasphorus-Rufus) - Effects of Relative Spacing Among Stimuli. *Journal of Comparative Psychology, 108,* 29-35.

Brown, G. S. and Gass, C. L. (1993). Spatial Association Learning by Hummingbirds. *Animal Behaviour, 46,* 487-497.

Cheng, K. (1986). A Purely Geometric Module in the Rats Spatial Representation. *Cognition, 23,* 149-178.

Cheng, K. and Spetch, S. M. (1998). Mechanisms of landmark use in mammals and birds.

Crawley, M. J. (2002). Statistical Computing: An Introduction to Data Analysis using S-Plus. New York: John Wiley and Sons Ltd.

Gould-Beierle, K. L. and Kamil, A. C. (1999). The effect of proximity on landmark use in Clark's nutcrackers. *Animal Behaviour, 58,* 477-488.

Healy, S. D. and Hurly, T. A. (1998). Rufous hummingbirds' (Selasphorus rufus) memory for flowers: Patterns or actual spatial locations? *Journal of Experimental Psychology-Animal Behavior Processes, 24,* 396-404.

Hurly, T. A. and Healy, S. D. (2002). Cue learning by rufous hummingbirds (Selasphorus rufus). *Journal of Experimental Psychology-Animal Behavior Processes, 28,* 209-223.

Iwai, E., Yaginuma, S., and Mishkin, M. (1986). Acquisition of Discrimination-Learning of Patterns Identical in Configuration in Macaques (Macaca-Mulatta and Macaca-Fuscata). *Journal of Comparative Psychology, 100,* 30-36.

Jacobs, L. F. and Schenk, F. (2003). Unpacking the cognitive map: The parallel map theory of hippocampal function. *Psychological Review, 110,* 285-315.

Jones, J. E., Antoniadis, E., Shettleworth, S. J., and Kamil, A. C. (2002). A comparative study of geometric rule learning by nutcrackers: (Nucifraga columbiana), pigeons (Columba livia), and jackdaws (Corvus monedula). *Journal of Comparative Psychology, 116,* 350-356.

Muller, M. and Wehner, R. (1988). Path Integration in Desert Ants, Cataglyphis-Fortis. *Proceedings of the National Academy of Sciences of the United States of America, 85,* 5287-5290.

Pacini, E., Nepi, M., and Vesprini, J. L. (2003). Nectar biodiversity: a short review. *Plant Systematics and Evolution, 238,* 7-21.

Steck, S. D. and Mallot, H. A. (2000). The role of global and local landmarks in virtual environment navigation. *Presence-Teleoperators and Virtual Environments, 9,* 69-83.

Thiele, J. and Winter, Y. (2005). Hierarchical strategy for relocating food targets in flower bats: spatial memory versus cue-directed search. *Animal Behaviour, 69,* 315-327.

Vargas, J. P., Lopez, J. C., and Thinus-Blanc, C. (2004). Encoding of geometric and featural spatial information by goldfish (Carassius auratus). *Journal of Comparative Psychology, 118,* 206-216.

Winter, Y. and von Helversen, O. (2001). Bats as Pollinators: foraging energetics and floral adaptations. Pages 148-170 *in* L. Chittka and Thomson, J.D. eds. Cognitive ecology of pollination. Cambridge University Press, Cambridge.

Winter, Y., Von Merten, S., and Kleindienst, H. U. (2005). Visual landmark orientation by flying bats at a large-scale touch and walk screen for bats, birds and rodents. *Journal of Neuroscience Methods, 141,* 283-290.

Chapter 3

Foraging on nectar: A flower visiting bats ability to perceive differences in nectar volume

Abstract

One aspect of floral quality is the volume of nectar produced, and nectar feeding animals must be able to estimate the volume received from a flower to assess flower quality. In this study we examined the ability of flower visiting neotropical bats *Glossophaga soricina* to discriminate between two nectar volumes. We applied a two-alternative forced-choice paradigm. Results are presented as a psychometric function implying that bats possess a well developed sense for the perception and discrimination of volumes of nectar.

Introduction

FORAGING DECISIONS OF animals that feed on nectar are influenced by many physiological and environmental factors. Without doubt, the amount and quality of the nectar reward play a dominant role as one of these factors (Shettelworth 1998). Bumblebees, as one example, readily return to patches of flowers with high nectar secretion rates, and thereby avoid poorer patches (Cartar 2004). Thus, differences in available nectar volumes may immediately effect foraging decisions of nectarivores and underlying this must be a general ability of nectar feeding animals to judge the quality of a flower by estimating the nectar content (Garrison and Gass 1999, Thomson 1988, Stout & Goulson 2002, Robertson et al. 1999)

The ability of an animal to discriminate between differing physical stimuli (here nectar volume) is directly related to the intensity of the single stimuli. This relationship is expressed by the Weber-Fechner law, which states that the just noticeable difference between two physical stimuli increases in proportion with increasing intensity of the two single stimuli. This is also known as the scalar property in psychophysics.

Here, we determined the psychometric function for perceiving nectar volumes for the neotropical flower-visiting bat, *Glossophaga soricina*, a species that is well suited for investigating decision making, foraging behaviour, and cognitive ecology in mammals. For this we determined responses to differing volumes of sugar solution in a two alternative forced choice paradigm (2AFC), while offering volumes similar to those found under natural conditions (Winter & von Helversen 2001). The data was analysed by fitting a psychometric function.

The psychometric function relates the subjective (psychological) reaction of the animal to the physical stimulus intensity. Here, the threshold (the highest slope of the function) denotes the stimulus intensity at which bats could clearly distinguish between the two stimuli. This is to our knowledge the first application of this rigorous and standardised method to quantify the ability to distinguish between two volumes. The advantage of this procedure is that it permits not only a qualitative evaluation as to whether an animal can distinguish between two options, but also that it results in a quantitative, formal model of underlying perceptive abilities.

Materials and Methods

Animals

Seven bats of the species Glossophaga soricina (Phyllostomidae) bred in captivity were used for this study. The climatic conditions both in the animal holding facility and in the experimental room were 22°C and approx. 60% rel. humidity. The diet consisted of 17% honey water, to which Nektar Plus or Nutricomp were added in addition dry pollen. Artificial nectar from experimental food dispensers was a 17% sugar solution made from sucrose, glucose and fructose in equal parts as found in the nectar of bat visited flowers (Baker et al. 1998). Light conditions were LD 12:12 and all experiments with the echo locating bats were conducted during the scotophase.

Experimental apparatus

During the experiments bats were kept individually in cages (0.7 m X 2.2 m X 1.5 m). Inside the cages two feeders were installed on the back wall. Feeders had a cylindrical PVC opening equipped with a photoelectric barrier to automatically detect visiting bats. For a reward, a valve at the backside of the cage opened with an audible click and a syringe pump delivered a variable amount (see experimental protocol) of odourless nectar to the base of the feeder opening, which bats removed by licking (Winter and von Helversen 2001). Swivel arms mounted above each feeder allowed each feeder to be closed by moving a plastic flap in front of its opening. Details of the experimental apparatus are given in Winter and Stich (2005).

Pre-Training

All bats received two days of training in their individual cages to accustom them to the experimental surroundings. We helped bats find and use the feeders by applying a drop of honey to the tip of each feeder on the first pre-training day. All bats used in this experiment quickly found the feeders and visited them regularly. During pre-training, feeders delivered 30 µl of sugar water solution on each visit to a feeder. On the second night bats had to visit the feeders in alternation to prevent them from developing a spatial preference to a single feeder. This was done by automatically moving a flap in front of the just visited feeder and simultaneously opening the other feeder by means of rotating the swivel arms.

Experimental procedure

We tested the bats in a modified two alternative forced choice paradigm (2AFC). The two feeders in the cage provided the bat with differing amounts of nectar solution. One trial consisted of 50 visits to the feeders and was divided into two phases. In the first phase, the sample phase, bats had to visit feeders in alternation for 20 visits (10 visits to each feeder). In this phase the flaps automatically moved in front of a feeder to ensure that no unrewarded visits to a feeder could occur. In the second phase, the choice phase, bats could choose freely between the two different amounts (feeders). This phase lasted for thirty visits. Trials with different pairings of two amounts followed in direct succession.

We presented bats with a total of 8 combinations of different volumes (Table 3.1). Preliminary experiments had suggested that the threshold for discrimination should be somewhere below 1.5, thus we aimed with our selection of combinations at having many values below 1.5, and only two values above 1.5. Each combination of volumes was offered twice, such that during one trial the higher volume was on the right, during the other trial it was on the left to correct for spatial biases of the bats.

Table 3.1: Sugar solution volumes presented to bats at the two feeders. Each volume was tested twice with alternating sides. For calculation of the stimulus intensity see text.

Volume 1 (µl)	***Volume 2 (µl)***	***Stimulus intensity***	***Median of reaction to stimulus***	***Standard deviation of reaction to stimulus***
21	24	0.143	0.56	0.22
24	30	0.25	0.56	0.08
6	9	0.5	0.73	0.16
12	18	0.5	0.68	0.16
9	15	0.67	0.67	0.2
9	21	1.33	0.77	0.17
6	24	3	0.85	0.12
3	27	8	0.91	0.09

Psychometric function

For the estimation of the psychometric function we pooled the data from all seven bats and applied the algorithm proposed by Kuss et al. (2005). Stimulus intensities were calculated by dividing the difference between the two volume stimuli by the volume of the lower stimulus (Table 3.1). We fitted a logistic psychometric function to the data following the detailed instruction in

Kuss et al. (2005). This recently developed algorithm will estimate the psychometric function and three important parameters of this function with their confidence intervals. The first parameter (threshold parameter) is the point at which the investigated subject can distinguish between the two stimuli and is denoted by the point on the psychometric function with the steepest slope. The second parameter is the slope at this point, which gives a measure for the reliability of sensory performance (Treutwein & Strassburger 1999). The third parameter is the lapse rate, which is inferred from the difference between perfect performance and the actual behaviour of animals at high stimulus intensities. It serves as a measure for the errors that are not of perceptional nature but are made due to lapses in attention or motivational problems. Markov Chain Monte Carlo (MCMC) sampling is applied for an estimation of these parameters. In this Bayesian approach to find the parameter estimates, the investigator has to state his/her prior beliefs about the parameter location in form of prior distributions. As prior functions we chose a beta distribution (2,50) for the lapse rate, normally distributed priors for the threshold, and the slope with a mean of 0 and a standard deviation of 1. For the MCMC sampling we performed 5000 runs with 50 leapfrog steps each. The leapfrog step size for the three parameters were: 0.05 (lapse rate), 0.08 (threshold location), 0.1 (slope) (the acceptance rate was at approximately 82%).

Results

Individual bats completed 16 trials of 8 different volume pairs (Table 3.1) within two experimental nights. With 30 free choices per trial all bats made a total of 480 choices. The resulting psychometric function is given in Figure 3.1. As expected, bats showed an increasing preference for the larger volume as the stimulus intensity increased (Table 3.1). The threshold stimulus intensity at which bats could clearly discriminate between the two stimuli was at 0.77 with a 95 % confidence interval from 0.62 to 0.93. At this point the estimated slope was at 2.52 with a 95 % confidence interval from 1.91 to 3.27.

The lapse rate gives the approximate percentage that bats chose a feeder arbitrarily instead of directing their visits according to the stimulus intensity. This rate was given with 21 % (95 % confidence interval from 17.1 % to 25.2 %).

To check whether the scalar property was preserved for the investigated interval of volumes we compared the reactions at 0.5 stimulus intensity of two different volume combinations, one combination of low volumes (6 µl and 9 µl) and one combination of high volumes (12 µl and 18 μl). There was no significant difference between the reaction strengths to the two combinations (paired Wilcox test: W=30.5; P=0.48).

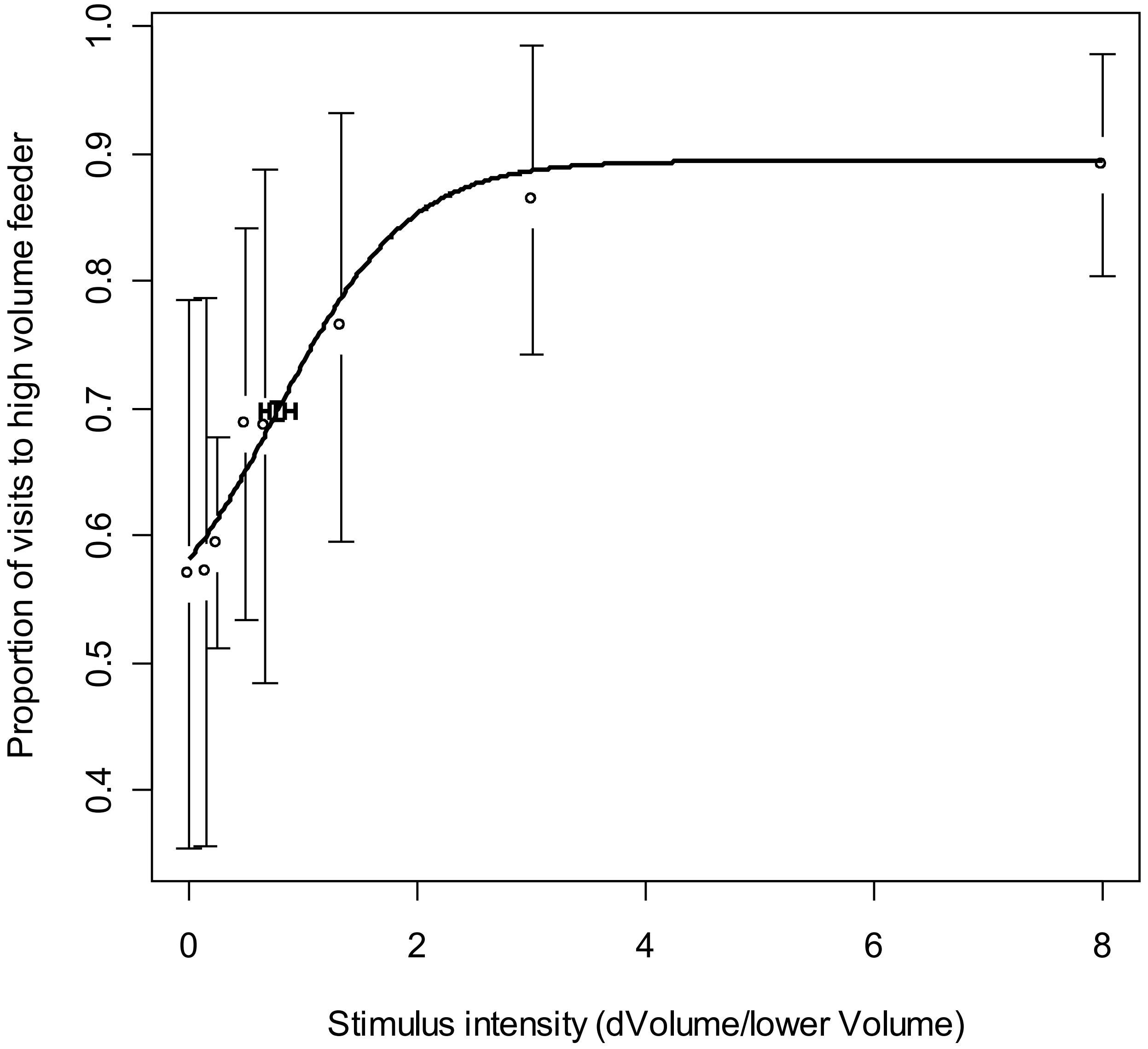

Figure 3.1: Psychometric function of discriminatory reaction of bats to stimulus intensities resulting from nectar volume differences. Abscissa shows the stimulus intensities and ordinate shows the percentage of visits to the feeder with higher sugar solution volume. The curve represents the estimated psychometric function with the box denoting the highest slope of the function (threshold) with error bars containing the 95 % confidence interval around the threshold.

Discussion

We used a 2AFC paradigm to determine the ability for fluid volume discrimination. Such an approach, to our knowledge, has not been used before for this purpose.

One of the assumptions underlying our paradigm for estimating a psychometric function is the preservation of the scalar property. The scalar property describes the phenomenon that an increase in intensity of two single stimuli will result in a proportional increase of the threshold at which the difference between the two stimuli can be detected. The difference in stimulus intensity is calculated as the relation of two single stimuli to each other. When changing the stimuli such that the relative difference is kept constant there should be no difference in the reaction to the two stimuli pairs. In our experiments this scalar property was preserved as the reaction of the bats to the pairs 6 µl, 9 µl and 12 µl, 18 µl of sugar water solution did not differ significantly (both pairs had a stimulus intensity of 0.5). At least for the interval we measured, bats behaved as predicted by the Weber-Fechner law.

However, even as the scalar property is preserved, estimates for threshold and slope could be influenced by the motivation of the bats to discriminate between the two stimuli. The motivation, or more general, the non perceptional errors that have been made by the bats were inferred from the estimate for the lapse rate. The lapse rate in this experiment was relatively high, as 20 % of the visits that did not mirror a decision that was influenced solely by the difference between the two stimuli. Moreover, bats had only 10 sampling visits to each feeder, which could result in an inexact estimate of what to expect at a particular feeder. It is thus possible that the threshold could lie lower than the estimated value, but under the given circumstances we obtained a robust conservative measure of the reaction to volume differences in *G. soricina*. Moreover, Klein (2001) points out that the lapse rate mainly influences the slope but not the threshold parameter that is estimated. Thus, this paradigm seems well suited to assess perceptional constraints, which severely influence decision-making in animals (Dukas 2004).

In the experiment bats showed a clear reaction in the given 2AFC task and adjusted their behaviour according to the differences between two given volumes of sugar solution. This resulted in an estimate of the threshold of 0.77. The following example will illustrate the meaning of this dimensionless value. A bat has the choice between two flowers. One will give 3 µl the other one 4 µl. In this case the bat will not be able to distinguish properly between the two flowers as 3 µl*1.77= 5.31 µl. Thus, one could expect an appropriate reaction to the difference between the two flowers from approximately 5 µl on such that bats will most likely visit the flower with the higher volume.

As mentioned in the introduction, studies on the ability of animals to discriminate between different volumes are rare and comparison is thus possible only in a limited way. What makes it even more difficult is that on the one hand the Weber coefficient is sometimes calculated slightly different from our approach. Shafir (2005) e.g. uses the mean of the two stimuli in the denominator instead of the lower stimulus. On the other hand we tested bats with a solution of three sugar components, which certainly makes a difference in water viscosity and thus could influence the sensory pathway. Nonetheless, the value for the threshold in this experiment seems to be lower for bats than for honeybees (*Apis melifera*). Shafir (2005) reports that bees were not able to discriminate correctly between 0.4 µl and 1.2 µl of a 1.5 M sucrose solution (34 % sugar solution w/w). This equals a Weber coefficient, as calculated in this study, of more than 2 for the bees, which is by far higher than the estimated 0.77 for bats.

The following implications arise from these results. First, future experiments with *G. soricina* that involve different nectar volumes should adopt their design to the boundaries of the sensory abilities of *G. soricina*.

Second, with more detailed psycho-physiological experiments in other nectar feeding species it will be possible to compare perceptional thresholds and draw conclusions about the importance of nectar volume for single species.

And third, not only the ability to discriminate between volumes is of importance for a decision making process in nectariviores. Dukas (2004) points out that the first constraint an animal faces when gathering information about its environment is a perceptional one. Thus further quantitative knowledge about the perceptional abilities of animals as gathered here will make up an important support for our explanations of animal behaviour.

Literature

Cartar, R. V. (2004). Resource tracking by bumble bees: Responses to plant-level differences in quality. *Ecology, 85,* 764-2771.

Dukas, R. (2004). Evolutionary biology of animal cognition. *Annual Review of Ecology Evolution and Systematics, 35,* 347-374.

Garrison, Jennifer S. E. and Gass, Clifton Lee. (1999). Response of a traplining hummingbird to changes in nectar availability. *Behavioral Ecology, 10,* 714-725.

Klein, S. A. (2001). Measuring, estimating, and understanding the psychometric function: A commentary. *Perception &*

Psychophysics, 63, 1421-1455.

Kuss, M., Jakel, F., and Wichmann, F. A. (2005). Bayesian inference for psychometric functions. *Journal of Vision, 5,* 478-492.

Robertson, A. W., Mountjoy, C., Faulkner, B. E., Roberts, M. V., and Macnair, M. R. (1999). Bumble bee selection of Mimulus guttatus flowers: The effects of pollen quality and reward depletion. *Ecology, 80,* 2594-2606.

Shafir, S., Menda, G., and Smith, B. H. (2005). Caste-specific differences in risk sensitivity in honeybees, Apis mellifera. *Animal Behaviour, 69,* 859-868.

Shettleworth, S. J. (1998). Cognition, Evolution, and Behavior. New York: Oxford University Press.

Stout, J. C. and Goulson, D. (2002). The influence of nectar secretion rates on the responses of bumblebees (Bombus spp.) to previously visited flowers. *Behavioral Ecology and Sociobiology, 52,* 239-246.

Thomson, J. D. (1986). Pollen Transport and Deposition by Bumble Bees in Erythronium - Influences of Floral Nectar and Bee Grooming. *Journal of Ecology, 74,* 329-341.

Treutwein, B. and Strasburger, H. (1999). Fitting the psychometric function. *Perception & Psychophysics, 61,* 87-106.

Winter, Y. and Stich, K. P. (2005). Foraging in a complex naturalistic environment: capacity of spatial working memory in flower bats. *Journal of Experimental Biology, 208,* 539-548.

Winter, Y. and von Helversen, O. (2001). Bats as Pollinators: foraging energetics and floral adaptations. Pages 148-170 *in* L. Chittka and Thomson, J.D. eds. Cognitive ecology of pollination. Cambridge University Press, Cambridge.

Chapter 4

Investigating the impact of ecology upon the timing ability in animals

- testing a flower-visiting bat in the peak procedure.

Abstract

Several species (pigeons, rats) have already been tested in the so-called peak procedure for their ability to estimate small time intervals. A comparison of these species with regard to the precision of their respective timing ability has not been undertaken until now. However, as with other cognitive abilities. the ability to time intervals could underlie evolutionary pressures that will enable species that face special temporal demands in their environment to have especially fine tuned time senses. We investigated this hypothesis here by testing a Neotropical bat, *Glossophaga soricina*, that visits flowers in two fixed interval schedules. Bats showed the same summed response distribution for so-called empty trials as other species. When investigating single trials, bats showed higher precision in their ability to time small intervals in comparison to other species This effect, however, was overshadowed by high variation in precision within species. Without testing further species we cannot conclude that there is an impact of ecology upon the precision of the timing ability in animals.

Introduction

THE TIMING BEHAVIOUR of animals has received much attention over the last decades. One approach to investigate the mechanisms of timing behaviour has been so-called fixed interval (FI) paradigms. Here, animals are trained via reinforcement to delay their response to a conditioned stimulus for a fixed time interval. An extension of such a paradigm is the peak procedure (Catania 1970). After an animal has established a stable reaction to the trained time interval, so-called empty trials are interspersed with normal FI trials. On empty trials no reinforcement is given and the response of the animal continues beyond the time point previously experienced with a reward. Results from various studies (Roberts 1981, Rakitin et al. 1998, Cheng and Roberts 1991, Brodbeck et al. 1998, Rodriguez-Girones and Kacelnik 1999) show symmetrical response rates distributed around the FI time. The peak of the response is lying near or directly at the FI time. With an increasing FI time the standard deviation (i.e. spread of distribution around the peak) also increases, in accord with Weber's Law (Gibbon and Church 1990).

The spread of the distribution around the FI time is caused by a so-called break-run-break pattern that can be observed in single trials of individuals. Here, subjects change behaviour abruptly from a low rate (break) to a high rate (run) of responding. At the end of the run the behaviour again changes abruptly to a low rate (Gibbon & Church 1990, Cheng & Westwood 1993, Church et al. 1994, Brodbeck 1998).

The scalar expectancy theory (SET) (Gibbon & Church 1984) is the most influential model to account for theses results. It consists of three components; first, an interval clock that measures elapsed time; second, a memory for time intervals and thresholds; and third, a decision component that integrates the information from clock and memory. In short sampling intervals this integrator will compare the memory with the interval clock and when the difference between the two drops below a threshold the run phase will start. For stopping the run phase, a second memory content is compared to the interval clock and, again, when the difference between memory and clock falls under a certain threshold, the run phase stops.

Several studies have investigated animals' ability to time intervals with respect to SET. However, there has been little research on the quality of interval timing when comparing several species. Just as with other cognitive abilities, like spatial memory (Krebs et al. 1996), the precision of interval timing could be correlated with the requirements of an animal's environment. Thus, species that are in need of precise interval timing should show increased performance in the peak procedure.

But what does increased performance mean in this context? Several factors could describe the precision in such a system. First, consider the precision of the peak with regard to the FI time. If the maximum response of an animal lies directly at the FI time, the precision to time intervals is high. However, the maximum peak response is only based upon the single trials that exhibit a break- run-break pattern. A better measure for the precision of an animal could be the start of the run phase in relation to the peak interval time. According to SET, a run is initiated when the difference between the interval clock (accumulator) and the reference memory falls below a certain threshold. This threshold depends upon the rate at which the accumulator and the interval clock are compared to each other. A lower rate will lead to higher thresholds a higher rate will lead to lower thresholds. A higher rate in the comparator might enable an animal to start later with the run phase and save energy or time.

In this study we investigated the response of a flower-visiting Neotropical bat, *Glossophaga soricina*, to two different FI schedules. For a species that forages on spatio temporally predictable resources like floral nectar, where flowers replenish their nectar content within short time intervals, the ability to estimate time intervals seems to be an important prerequisite to optimise the timing of foraging visits to individual resource locations. We compared the behaviour of the bats in the peak interval task with the behaviour of other species in similar tasks to investigate the possibility that the ecology of an animal has a direct impact upon the precision of interval timing. For this we compared the start times of a run in relation to the peak interval time estimated between different species. If the speed of the comparator were faster in bats, we would expect to find a later start of the run phase in bats than in rats for example .

Materials and methods

Animals

Twelve bats of the species *Glossophaga soricina* (Phyllostomidae) bred in captivity were used for this study. The climatic conditions both in the animal keeping facility and in the experimental room were 22°C and approx. 60% rel. humidity. The diet consisted of 17% honey water to which Nektar Plus or Nutricomp was added in addition dry pollen. Artificial nectar from experimental food dispensers consisted of a 17% sugar solution made from sucrose, glucose and fructose in equal parts as found in the nectar of bat-visited flowers (Baker et al. 1998). Light conditions were LD 12:12

and all experiments with the echo-locating bats were conducted during the scotophase.

Experimental apparatus

During the experiments bats were kept individually in cages (0.7 m X 2.2 m X 1.5 m) in total darkness. Inside the cages two feeders were installed on the back wall. Feeders had a cylindrical PVC opening equipped with a photo-electric barrier to detect visiting bats automatically. For a reward, a valve at the backside of the cage opened with an audible click and a syringe pump delivered a variable amount (see experimental protocol) of odourless nectar to the base of the feeder opening, which bats removed by licking (Winter & von Helversen 2001, Winter & von Helversen 2003). Swivel arms mounted above each feeder allowed for closing each feeder by moving a plastic flap in front of its opening. Details of the experimental apparatus are given in Winter and Stich (2005).

Experimental procedure

We established the fixed interval peak procedure in a modified paradigm by providing bats with two feeders that could be closed individually with a plastic flap. One feeder served as the trigger feeder and one feeder served as the peak feeder. At the beginning of each peak trial the trigger feeder was open and the peak feeder was closed by the flap. A green LED at the tip of the trigger feeder indicated that it was active. When the subject visited the trigger feeder, it received a reward of 6 µl. In this moment the trigger feeder closed and the peak feeder opened and the LED at the tip of the peak feeder went on. Moreover, opening the flap was associated with a motor-generated noise audible to the bats and with a change in the echo-acoustic appearance of the feeder opening that could be sensed by the echo-locating bats. The bat was now free to visit the peak feeder, however, only after the FI had elapsed could the bat receive a reward of 45 µl. The reward could be obtained in the time interval between FI and FI*1.5 after visiting the trigger feeder. When the bat did not visit in this time interval, the peak feeder remained open for FI*3. 20 % of all trials were so-called empty trials where no reward was given. Here, the feeders remained open for FI*3. The start of a new trial was always initiated by the animal visiting the trigger feeder after it had opened.

We tested bats on two FI schedules. We divided the twelve bats into two groups of six bats. One group accomplished a 5 s FI schedule and the other an 11 s FI schedule.

Pre-Training

All bats received five days of prior training in their individual cages to accustom them to the experimental surroundings. We helped bats find feeders by olfaction by applying a drop of honey to the tip of each feeder on the first pre-training day. All bats used in this experiment quickly found the feeders and visited them regularly. During training feeders delivered 30 µl of sugar water solution on each visit to a feeder. On their second night bats had to visit the two feeders in alternation to prevent them from developing a spatial preference to a single feeder. This was done automatically by moving a flap in front of the feeder just visited and simultaneously opening the other feeder by means of rotating the swivel arms.

On the third training day we introduced the peak interval procedure as described in the experimental procedure. The only difference between the two schedules was the time interval that lapsed before a reward was delivered. On the third training day bats received a reward from FI until FI*3, on the fourth day from FI to FI*2, and on the fifth training day received a reward from FI to FI*1.5. During training no empty trials, trials without reward, occurred.

Data Analysis

We used only the data from empty trials for analysis. The maximum peak response rate was calculated for each animal by the iterative method described by Cheng and Westwood (1993). Here, an initial first median (m_1) was calculated from all time intervals of all visits of one animal to the peak feeder since the onset of the signal (opening of the flap after visit to trigger feeder). Then the next value for the median (m_i) was calculated in the interval 0 until $m_{i-1}*2$. This was repeated until $m_{i-1}-m_i < 1$ ms. The final median denoted the time interval after which the highest response was exhibited by the bats. Throughout the whole manuscript we give the median and the median adjusted deviation.

Results

All bats acclimated well to the situation in the cage and found both feeders during the first training night. Bats also were trained easily to alternate between the two available feeders on the second day of training. All bats accomplished the five-day pre-training without problems.

During the experimental nights bats performed 420 ± 128 empty trials in each treatment (5 s and 11s peak interval time). For all following analyses we excluded the first 50 empty trials to ensure that the behavioural reaction to the FI time was not influenced by the first onset of empty trials.

Empty trials consisted of 2.7 ± 1.6 (5 s FI) and 4.5 ± 1.7 (11 s FI) visits to the peak feeder with no significant difference between the two schedules (Wilcoxon sum rank test: W=11, P=0.31, N=12). The peak time interval for bats in the 5 s FI schedule was 6.3 s ± 0.2 s (Figure 4.1 a, Table 4.1). In the 11 s FI schedule the peak time interval amounted to 12.3 s ± 2.0 s (Figure 4.1 b, Table 4.1). Both graphs for the 5 s and 11 s FI schedule in figure 4.1 show the strongest reaction slightly later than the FI time and both also show a smaller peak at 2 s.

Table 4.1: Revisit time intervals for the two FI schedules (5 s and 11 s). Note that 12 animals took part in the experiment and that the observation column gives the observation number for each separate FI schedule.

Observation	***Peak time FI 5 s (s)***	***Peak time FI 11 s (s)***
1	6.2	14.0
2	6.3	10.6
3	6.5	12.2
4	8.0	12.4
5	6.2	15.7
6	5.7	11.3

To test whether the scalar property was preserved across the two FI schedules, we plotted the relative reaction strength at a certain time interval against quintiles of the FI time. This resulted in a normalised plot with the onset of the reward interval at 5 and the end of the reward interval at 7.5 regardless of the FI time. The two graphs of the two FI schedules superimposed each other, although the peaks were at 7 (5s FI) and at 6 (11s FI), which led to a slightly negative skew for the graph of the 5 s FI schedule.

To investigate whether the spread of the distribution of points in time of feeder visits was caused by a break-run-break pattern as in other species, we calculated the median of the revisit intervals for the first visit after the onset of the signal (flap opening) and the time intervals between all other successive visits during one empty trial. If a break-run-break pattern was exhibited, the time interval before the first visit occurred should have been greater than the time intervals between the following visits in the trial.

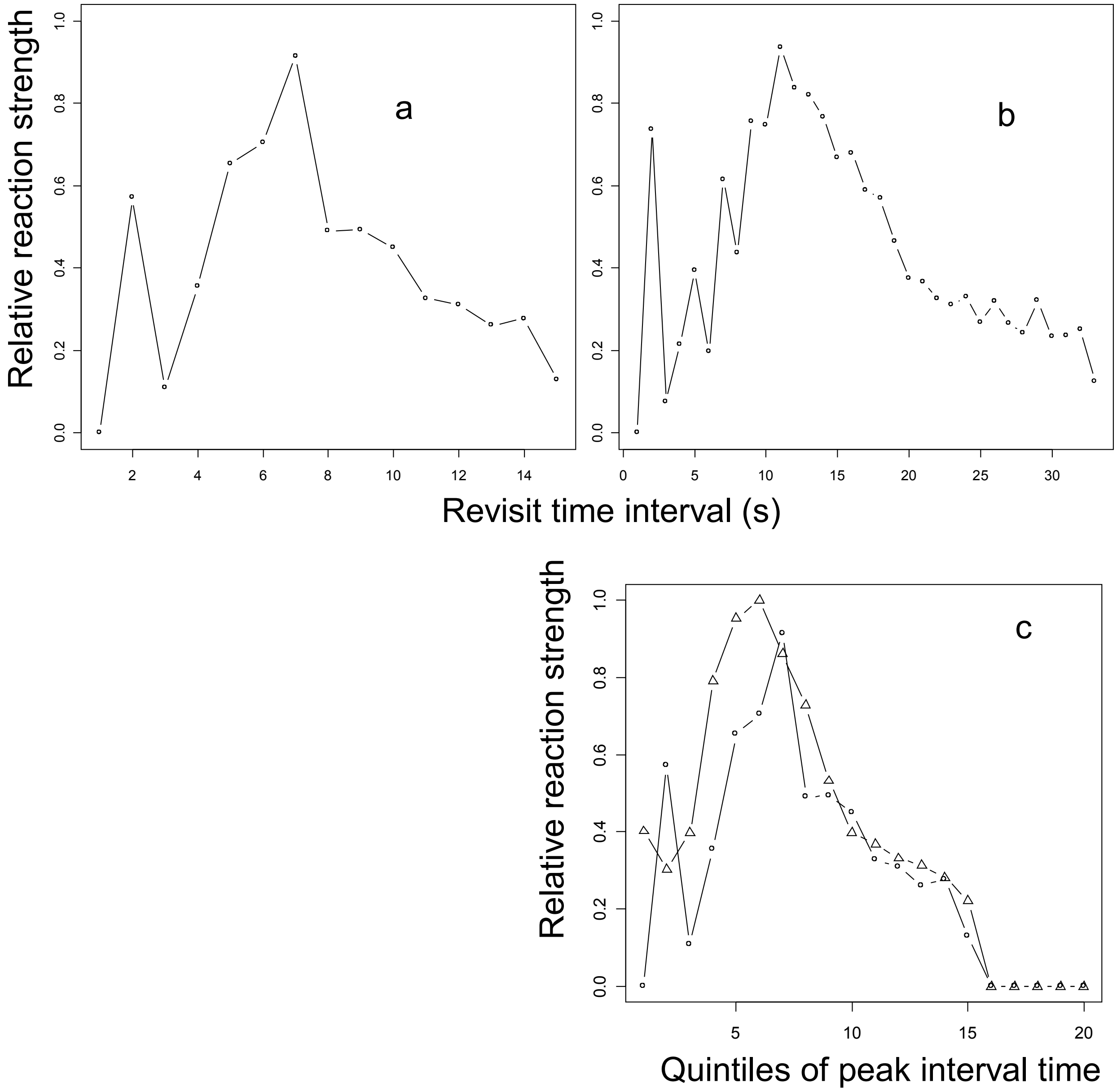

Figure 4.1: Summed response distributions of empty trials for bats tested on FI 5 s (a, n=6) and FI 11 s (b, n=6) peak procedure and normalised summed response distributions relative to FI time. Abscissa shows time in seconds (a,b) or relative time in quintiles of FI time (c). Ordinate shows the response strength of all animals at each point in time relative to the maximum response strengths. Graphs are summed responses for all bats showing the median of the summed response distributions of individual bats.

The first visit after the onset of the signal occurred in the 5 s FI schedule after 4.7 s ± 1.5 s. The time interval between the next visits until the end of the trial amounted to 2.3 s ± 1.3 s. The time interval before the first visit occurred was significantly greater than the time interval between successive visits in the 5 s FI schedule (Wilcoxon one sided, paired, signed rank test: V=21; P<0.05; N=6). In the 11s FI schedule the first visit occurred after 7.3 s ± 2.3 s and the next visits occurred after 2.5 ± 0.5 s with a significant difference between the two (Wilcoxon one sided, paired, signed rank test: V=20; P<0.05, N=6).

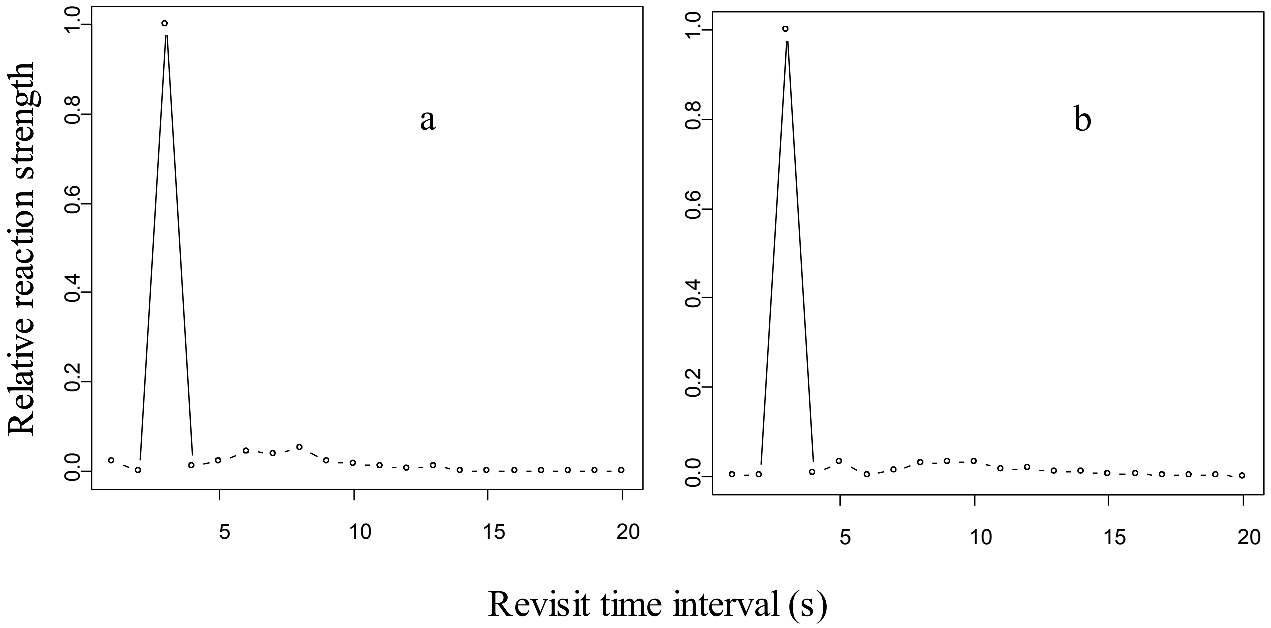

Figure 4.2: Distribution of revisit time intervals for FI 5 s (a) and FI 11 s (b) peak interval procedure for all revisits after the first visit to the peak feeder. Ordinate shows the response strength at each point in time relative to the maximum response strengths. Abscissa shows the revisit interval between two successive visits at the peak feeder in seconds.

When looking at the distribution of the revisit time intervals at the peak feeder after the first visit to the peak feeder, there are clear peaks at two seconds (Figure 4.2). Such peaks were common to all animals in both FI schedules.

Discussion

Bats reacted to the given FI schedules in a manner similar to that found in other studies for different species (e.g. Cheng & Westwood 1993, Brodbeck 1998, Church et al. 1994). When trained on the peak procedure, bats showed a peak in response behaviour near the FI time. The spread of the distributions was proportional to the length of the FI time so that the distributions superposed when adjusted to the durations of the two different FI schedules. Bats had longer peak time intervals than rats and pigeons but about the same values as black-capped chickadees (Table 4.2).

As in the other studies, bats showed abrupt bursts of activity after visiting the peak feeder for the first time in individual trials. Thus, the reaction on a single trial level to the FI schedule was, as in other species, not a steady increase as suggested by the average distribution (Figure 4.1) but a fast increase in activity. Here, we could show that the revisits after the beginning of a run are evenly spaced and animals aim for high frequencies in their visitation pattern at the peak feeder, exhibiting the typical run-break-run pattern. In the case of the bats this high frequency was at one visit per 2 s, which we believe could be even higher but in the small cage with lots of flight manoeuvres necessary to return to the feeder, this value is at the upper limit. However, in a larger cage this value could be even lower.

Table 4.2: Comparison of peak times and start times for runs for pigeons (Cheng and Westwood 1993), black capped chickadees (Brodebeck et al. 1998), rats (Church et al. 1994) and bats (this study).

Animal	***FI schedule (s)***	***Peak time (s)***	***Start of run (s)***	***Start of run/Peak time***
Pigeons	12.5	11.6	5.62	0.48
Chickadees	12.5	15.8	10.07	0.67
Chickadees	37.5	41.41	17.9	0.43
Rats	15	15	6.5	0.43
Bats	11	12.3	7.3	0.59
Bats	5	6.3	4.7	0.74

In this study we especially were interested in whether the special foraging ecology of *G. soricina* had an impact upon precision in the ability to time small intervals. Here, the speed of the comparator plays a special role as a faster comparator will enable bats to delay the start of the run phase and ultimately make fewer visits to the peak feeder before reinforcement. To measure the rate of the comparator, we related the start times of four species (pigeons, rats, black capped chickadees and bats) to the peak interval time. The peak interval time, here, denotes the point in time the animals exhibit the strongest reaction during the FI schedule. It is thus the point in time the animals most probably expect a reward. But why is this point not exactly at the FI time for the bats?

During the FI schedule bats only received a reinforcement (reward) after the FI time elapsed. Bats could not show a continuous response after the signal onset as in other paradigms. Bats needed to perform a hovering flight in front of the feeder in order to stick their snout into the feeder opening. This hovering flight is normally maintained for much shorter than 2 s (Winter 1998). After this, bats had to leave the feeder and revisit after approximately 2 s. Thus, when visiting the peak feeder just before the FI time had elapsed the bat would receive an reinforcement 2 s after the FI time which led with most bats to a peak time later than the FI time (Table 4.1).

However, this does not imply that bats were more imprecise in their timing than rats or pigeons. When comparing the ratio of the start times for the run phase and the peak interval time (table 2) between the animals, bats have slightly higher ratios than rats or pigeons. Bats start their run phase in the 5 s FI schedule after 4.7 s, which is only 300 ms below the FI time. If all animals had the same quality in their timing mechanism, the ratio between start of run phase and peak interval time would have been all the same according to Weber's Law. However, bats show much higher ratios than pigeons or rats, which have similar values. Moreover, there is a difference in the ratio between the 5 s FI schedule and the 11 s FI schedule within bats, with the 5 s FI schedule ratio being much higher than the 11 s FI schedule. The same pattern can be found in black-capped chickadees for 12.5 s and 37.5 s. At this point the picture is not very consistent for the species we looked at. There are differences between species. However, these differences cannot be said to be significant as the number of species we looked for at this level of detail is still very low and the differences within species between different conditions are also quite high. The impact of ecology on the ability to time small intervals is not yet clear. Brodbeck et al. (1998) had similar doubts about their results but argued that the low number of animals (n=3) was responsible for the inconsistent picture within species as well as in comparison to rats. In this study, however, we had six subjects yet the behaviour in single trials at longer time intervals was not consistent with the behaviour in smaller time intervals and there were deviations from other species.

Yet, the short FI schedules in which animals are tested in the peak procedure often are ecologically not relevant. The attempt to detect differences resulting from an ecological evolutionary context thus might fail here and only the investigation of longer time intervals will reveal deeper insights. Nonetheless, bats of the species *Glossophaga soricina* queue into the line of animals like pigeons (Cheng & Roberts 1991), rats (Church et al. 1994), hens (Taylor et al. 2002), starlings (Rodriguez-Girones & Kacelnik 1998), mice (Gallistel et al. 2004), chickadees (Brodbeck et al. 1998), goldfish (Drew et al. 2005) and humans (Rakitin et al. 1998), which possess the ability to time small intervals. This general ability can be explained with similar models, implying a possible general mechanism.

Literature

Baker, H. G., Baker, I., and Hodges, S. A. (1998). Sugar composition of nectars and fruits consumed by birds and bats in the tropics and subtropics. *Biotropica, 30,* 559-586.

Brodbeck, D. R., Hampton, R. R., and Cheng, K. (1998). Timing behaviour of black-capped chickadees (Parus atricapillus). *Behavioural Processes, 44,* 183-195.

Catania, A. C. (1970). Reinforcement schedules and psychophysical judgements: A study of some temporal properties of behavior. 1-42.

Cheng, K. and Roberts, W. A. (1989). 3 Psychophysical Principles in Pigeon Timing. *Bulletin of the Psychonomic Society, 27,* 529-529.

Cheng, K. and Westwood, R. (1993). Analysis of Single Trials in Pigeons Timing Performance. *Journal of Experimental Psychology-Animal Behavior Processes, 19,* 56-67.

Church, R. M., Meck, W. H., and Gibbon, J. (1994). Application of Scalar Timing Theory to Individual Trials. *Journal of Experimental Psychology-Animal Behavior Processes, 20,* 135-155.

Drew, M. R., Zupan, B., Cooke, A., Couvillon, P. A., and Balsam, P. D. (2005). Temporal control of conditioned responding in goldfish. *Journal of Experimental Psychology-Animal Behavior Processes, 31,* 31-39.

Gallistel, C. R., King, A., and McDonald, R. (2004). Sources of variability and systematic error in mouse timing behavior. *Journal of Experimental Psychology-Animal Behavior Processes, 30,* 3-16.

Gibbon, J. (1977). Scalar Expectancy-Theory and Webers Law in Animal Timing. *Psychological Review, 84,* 279-325.

Gibbon, J. and Church, R. M. (1990). Representation of Time. *Cognition, 37,* 23-54.

Rakitin, B. C., Gibbon, J., Penney, T. B., Malapani, C., Hinton, S. C., and Meck, W. H. (1998). Scalar expectancy theory and peak-interval timing in humans. *Journal of Experimental Psychology-Animal Behavior Processes, 24,* 15-33.

Roberts, S. (1981). Isolation of An Internal Clock. *Journal of Experimental Psychology-Animal Behavior Processes, 7,* 242-268.

Rodriguez-Girones, M. A. and Kacelnik, A. (1999). Behavioral adjustment to modifications in the temporal parameters of the environment. *Behavioural Processes, 45,* 173-191.

Taylor, P. E., Haskell, M., Appleby, M. C., and Waran, N. K. (2002). Perception of time duration by domestic hens. *Applied Animal Behaviour Science, 76,* 41-51.

Voigt, C. C. and Winter, Y. (1999). Energetic cost of hovering flight in nectar-feeding bats (Phyllostomidae : Glossophaginae) and its scaling in moths, birds and bats. *Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology, 169,* 38-48.

Winter, Y. (1998). Energetic cost of hovering flight in a nectar-feeding bat measured with fast-response respirometry. *Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology, 168,* 434-444.

Winter, Y. and Stich, K. P. (2005). Foraging in a complex naturalistic environment: capacity of spatial working memory in flower bats. *Journal of Experimental Biology, 208,* 539-548.

Winter, Y. and von Helversen, O. (2001). Bats as Pollinators: foraging energetics and floral adaptations. Pages 148-170 *in* L. Chittka and Thomson, J.D. eds. Cognitive ecology of pollination. Cambridge University Press, Cambridge.

Winter, Y. and von Helversen, O. (2003). Operational tongue length in phyllostomid nectar-feeding bats. *Journal of Mammalogy, 84,* 886-896.

Chapter 5

Cognitive abilities in complex environments: Flower-visiting bats and the assessment of nectar production rates.

Abstract

When animals forage on spatio-temporally predictable resources like floral nectar, the resource renewal rate can be so high that revisits after short time intervals can be profitable. Here, the cognitive ability to assess the momentary quality of such resources by evaluating the production rate would facilitate the possibility to optimise foraging behaviour. The quality of such a resource is given by the renewal rate per time interval, that is, in the case of flowers, the amount of nectar that is produced in a given time interval. In this study we explored the cognitive abilities in a flower-visiting bat, *Glossophaga soricina*, that are involved to assess different secretion rates at six computer controlled artificial flowers. The emphasis lay on the question of what information from a particular feeder is used in the decision-making process of bats. We were particularly interested in whether bats can relate a food amount to a time interval that has passed in order to estimate resource production rate. The results showed that bats clearly responded to the differences in secretion rates by independently adjusting their revisit time intervals to each feeder with regard to the underlying secretion rate. To further investigate what mechanistic cognitive processes underlie this behavioural reaction, we developed several a priori mathematical models that simulated a hypothetical foraging bat that used different types of environmental information. The models differed in the quality of the memory stores for temporal information. The empirical data supported a model where bats were able to store several revisit time intervals at a flower and use these in conjunction with a reference memory for the amount gained at a flower in order to assess a resource production rate. The experimental results suggest that memory for several past time intervals can be employed by an animal in a decision process. Moreover, it is likely that the assessment of resource production rates, a prime requisite of optimal foraging theory, is possible via the found cognitive process.

Introduction

THE FORAGING ECOLOGY of an animal often has a strong impact upon the cognitive abilities and the development of underlying neuronal structures (Shettleworth 1998). The enlarged hippocampus of food storing birds (Healy & Krebs 1996, Krebs et al. 1996, Basil et al. 1996, Brodbeck 1994, Healy & Hurly 2004), the correlation between brain size and foraging ecology in cichlids (Huber et al. 1997), or the increased neostriatum size in birds that use tools for foraging (Lefebvre et al. 2002) are examples of how foraging ecology and the development of neural tissues and herewith associated cognitive abilities are related to each other.

In nature, animals that forage on renewable resources face a special situation that will demand special cognitive abilities. Examples for such patchily distributed renewing resources are floral nectar (Carthew and Goldingay 1997, Kamil 1978, Lemke 1984, Paton and Carpenter 1984, Ohashi and Thomson 2005), fruits (Janson 1998), foliage (Watts 1998), and prey in predator-prey (parasitoid-host) interactions (Briggs and Hoopes 2004). The problem that arises with renewing resources is that animals have to decide when to return to a resource location. This point in time will depend upon the energy that the animal has to invest to return to the patch and the renewal rate of the resource. Thus, an optimal solution to this trade-off problem would involve the cognitive ability to assess the renewal rate of a resource. And although the impact of learning and memory in these cases has been stressed (Krebs & Inman 1992; Hirvonen et al. 1999, Fortin 2002), evidence for an estimation and memory of an absolute rate has been scarce (Jaeger et al. 1982, Shettleworth & Plowright 1992, Cuthill 1990, 1994).

This might also relate to the fact that remembering several locations with an individual rate will require a great deal of computation. Thus, it might be feasible that foragers for renewable resources use simpler cognitive processes for decision making and apply heuristics or rules of thumb which will make use of only part of the information available (Todd & Gigerenzer 2000, Iwasa et al. 1981). The advantages lie in a faster and neurologically less expensive decision that will differ only slightly in (energetic) gain.

In the case of a renewable resource, the information that is available at a visit consists of two parts; first, the time interval since the last visit to the resource, and second, the amount of that particular resource that the animal harvested at this particular visit. The animals can use each of these factors in three ways. Either animals could ignore this factor (no memory hypothesis), use only the last information available on this factor (working memory hypothesis) or use several past experiences at the resource (reference memory hypothesis). Throughout the paper we will use the term working memory when only the last experience is stored in memory and use the term reference memory when several past experiences influence a memory content.

This study aimed at distinguishing between these three hypotheses by analysing empirical data and comparing this data to theoretical models that would account for the two factors, revisit time interval and amount of nectar, and the different usage of the information.

We investigated the reaction of a Neotropical bat, *Glossophaga soricina*, to linear nectar secretion rates at artificial flowers. This bat species shows specialised adaptations to visiting flowers (Dobat & Peikert-Holle 1985, Winter & von Helversen 2001). Here, we were particularly interested which information was employed by *G. soricina* at an artificial feeder to adapt to a reward pattern that was dependent upon temporal parameters.

Bats were confronted at first with an environment in which the six experimental feeders showed the same secretion rate. We then changed the secretion rates at the feeders. From this we would expect a change in revisit time intervals to the feeders such that a decrease in secretion rate would lead to longer revisit intervals and vice versa. Here, the transitory behaviour of animals following a change can give important insights into the nature of memory employed in a task. When reactions are only to immediate events, transition to asymptotic performance should be fast. On the other hand, when including past events in the decision process and thus relying on some kind of reference memory, transitions should be slow and asymptotic performance should be achieved only after several visits to the feeders. We investigated these two possibilities when conditions changed at the feeders.

To receive further insight to which factors influenced the decision to revisit a feeder, we compared the empirical data with several theoretical models. The models incorporated the two different types of information that can be obtained by a bat visiting a feeder, which are the revisit time interval and the amount of reward. We compared the empirical data to different scenarios of the model that involved different types of memory for the two factors (no memory, working and reference memory). The details and reasoning of the model are explained under a separate heading.

Thus, this study investigated whether or not, and how, bats could estimate the quality of a nectar resource by assessing the amount of nectar that is produced by a flower per unit of time. Moreover, we explored several theoretical possibilities of how the information obtained at a nectar resource is stored and integrated, and we compared the empirical data to these possibilities.

Materials and Methods

Animals

Six bats of the species *Glossophaga soricina* (Phyllostomidae) bred in captivity were used for this study. The climatic conditions both in the animal-keeping facility and in the experimental room were 22°C and approx. 60% rel. humidity. The diet consisted of 17% honey water to which Nektar Plus or Nutricomp was added, in addition to dry pollen. Artificial nectar from experimental food dispensers consisted of a 17% sugar solution made from sucrose, glucose and fructose in equal parts, as found in the nectar of bat-visited flowers (Baker et al. 1998). Before each nightly experiment bats received 2 ml of honey water with Nektar Plus (i.e. about 15% of daily intake). Light conditions were LD 12:12 and all experiments with the echo locating bats were conducted during the scotophase.

Experimental Setup

Experiments took place in a flight range (5.3 m X 8.7 m X 4 m) where bats could fly freely but also had a roost available. A rectangular feeder array was erected vertically at one end of the room. Feeders were arranged in an 8 by 8 rectangular configuration along the vertical plane with a distance of 0.4 m between each other. Only 6 and always the same feeders were active during the experiment. These feeders were indicated to the bats by echo acoustic stimuli (hollow sphere with holes, or training golf balls) that were presented directly above the feeders. This measure was taken to reduce the bat's visits to inactive feeders. Active feeders formed a hexagon with a side length of 0.8 m at top and bottom sides and 0.57 m at the other sides. The three feeders on the left and the three feeders on the right were separated by a board acting as a barrier with a depth of 0.4 m that stood perpendicular to the plane of the array.

Feeders had a cylindrical PVC opening equipped with a photo-electric barrier to automatically detect visiting bats. For a reward, a valve at the backside of the array opened with an audible click and a syringe pump delivered a predefined computer-controlled amount of odourless nectar to the base of the feeder opening, which bats removed by licking (Winter & von Helversen 2001). Each visit was recorded by a computer on the backside of the array with regard to the time of the visit, length of hovering duration, and how much nectar the bat received (for details of the method see Winter & Stich 2005).

Simulation of linear secretion rate and food availability

During the experiment bats were confronted with a temporal pattern of resource availability at the six feeders, which resulted from the simulation of nectar secretion rates of flowers in their natural environment. After a bat had collected sugar water from a feeder, a virtual account started on which the sugar water volume that could be received by the subject at this feeder increased with passing time. The relationship between elapsed time interval and amount of sugar water solution offered was linear. The only constraint to this was a lower value of 9 µl , and an upper limit of 60 µl which bats could receive from a single visit. However, if a flower contained e.g. 100 µl, a bat could visit twice and receive once 60 µl and then 40 µl on the second visit. Thus, no nectar when there was a long lapse between visits. By delaying the delivery of rewards after arrival of a bat at a feeder, bats had to hover for an average of 1000 ms when collecting a reward.

At the beginning of all experimental nights bats received 2 ml of initial starting amount of honey water that was given to them on a small dish. Together with the maximum amount of sugar water solution that could be obtained from the feeders during the experimental nights, bats were able to receive 11.5 ml per 12 h night. This amount ensured that they were mildly food deprived (Winter 1999).

Pre-Training

All bats were tested individually. Two days prior to the experiment, individual bats were introduced into the flight range. All six experimental feeders were active and at each visit bats received a reward of 15 µl. On the first day of pre-training, feeders were prepared with a drop of honey at the tip of each feeder so that bats could find all feeders. If it turned out that only one rewarding feeder was visited by the bat, the experimenter closed the opening of that particular feeder with adhesive tape. After bats had found all feeders and visited at least 50 times at each feeder, the tape was removed. This procedure ensured that bats knew of all feeders as potentially rewarding sites.

Experimental treatment

The experiment was divided into two phases with each phase lasting for two experimental nights of twelve hours each. During phase I the secretion rate was 120 µl per hour for all feeders, amounting to a maximum of 1.56 ml per feeder per 12 h night.

In the second phase of the experiment, secretion rates differed between the different feeders.

The secretion rates were increased by 50% up to 180 µl per hour at three feeders and rates were decreased by 50% to 60 µl per hour at the three other feeders. This changed food availability at single feeders but did not change the overall gain a bat could receive from the set of six feeders. Low and high secretion rate feeders were always in the same row but separated by the plastic divider described above.

Data analysis

Data analysis consisted of three separate steps. In the first step we were interested in how the time interval that had elapsed between two successive visits at the same feeder, the revisit time interval, depended upon the secretion rate, the treatment.

Beforehand we checked whether the different experimental nights could be compared. This was necessary because a difference in amount of sugar water solution a bat received and activity (visits to the set of six feeders in the 12 h of the experimental night) could have an impact upon revisit time intervals at individual feeders. For this comparison we computed two generalised linear models with both activity and the total amount of nectar gained as the dependent variables. We used GLMs with general estimating equations (GEE) (function geeglm; library geepack; R) to include the individual animals as repeated measures. Independent variables were phase (factors: single secretion rate at all six feeders, two different secretions rates) and night (factors: first night; second night in each phase). We assumed a poisson distribution for activity measured in visits per night (Crawley 2002). For the continuous positive dependent variable *total amount received per night,* we assumed a gamma distribution. We used the built-in link of the geeglm function.

After comparability of datasets had been established by the previous procedures, we compared revisit time intervals at the three different secretion rates as the first step of the data analysis. We modelled this by a Cox proportional hazards model (CoxPH) using the coxph function included in the survival library in R. The model included the *time interval between two visits at the same feeder* as the dependent variable and the type of secretion rate at this feeder (low, medium, high) as a factorial variable. We clustered the data by individual animals to correct for repeated measures and stratified for the number of visits each animal made at the feeders per experimental night as they were not independent of each other. This method is suggested by Clark et al. (2003). Due to the design of our study no censored data points occurred.

In a second step we analysed the data to search for components of the underlying learning process that led to an adaptation to the temporal task in this experiment. Here, we focused on the third experimental night, when for the first time the previously all equal feeders split up into three high secretion rate and three low secretion rate feeders. We looked at the development of revisit time intervals during this night and the proportion of rewards per visit in relation to total visits per feeder counted in blocks of ten visits. Analysis included fitting of GLMs with i. revisit time interval and ii. proportion of rewards per visit as dependent variables. We used GEEs to model repeated measures (function geeglm; library geepack; R). Each model included the independent variables course of the night given in blocks of ten visits (variable: counter_10) per feeder and the type of feeder (high, low) (variable: type) as factorial variable and their interaction.

The third step of our analysis compared the empirical data of the second nights of the two phases to several a priori models. The details of these models are given under a separate heading.

Throughout the manuscript we give the median rather than the mean and the median absolute deviation and not the standard deviation.

Theoretical models

Underlying a possible behavioural reaction to changing secretion rates at the feeders is a decision-making process that is influenced by several intrinsic and extrinsic factors. To investigate which factors might account for the observed behaviour, we conceptualised several theoretical models that were based on alternative hypotheses regarding the mechanisms underlying the assessment of sugar water secretion rates at experimental feeders. Within these models we investigated whether the empirical results, in form of distributions of revisit time intervals (second nights in phase one and two), could be explained by rather simple decision rules based on perceived food amounts, which did not include memory for time intervals, or if more intricate mechanisms, as the perception of time intervals and the integration of time intervals and received sugar water amount, were applied by the animals. Therefore, we simulated a hypothetical bat that will fly to one single feeder and ignored physiological constraints such as hunger, digestion and stomach content.

When visiting a feeder bats could obtain two types of information to direct their future decisions; first, the amount of sugar water they received and second, the time interval that has elapsed since the last visit at this feeder. We devised six hypotheses to divide up the different possibilities of using or neglecting this information.

Hypothesis 1 describes a basic possibility of how to solve the problem of visiting a flower with an underlying secretion pattern. This basic scenario assumes that a bat will revisit feeders at random time points without memory and consideration of previous revisit intervals. The total number of visits to a feeder is determined here by a 'rough' memory for the overall amount of received sugar water.

With hypotheses 2-6 we introduced an avoidance strategy by the bats for feeders which recently gave a reward. Winter and Stich (2005) showed that bats avoided feeders that recently delivered a reward. Two factors that relate to the two types of information that could be obtained when revisiting a feeder influence this avoidance. The first factor is the future revisit time interval to a feeder that a bat estimates in a situation. In this case, future describes the next revisit time interval at a certain feeder. This expression is chosen to distinguish from the revisit interval that lies in the past and has been experienced already. The future revisit time interval has to be estimated by the bats. The factor upon which this estimate is based differs between the hypotheses. Hypothesis 2 assumes that bats do not orient by a recently experienced revisit time interval, but have a fixed future revisit time interval. The method to calculate this fixed time interval from the empirical data is explained in the mathematical section. In hypothesis 3 and 4 the future revisit time interval depends upon a recently experienced revisit time. The future revisit time is determined by the last revisit interval experienced at a feeder in hypothesis 3 and the time interval since the last reward at a feeder in hypothesis 4. In hypothesis 5, bats possess a memory for revisit time intervals experienced in the past. An integration of these past revisit interval times will determine the future revisit time interval, which also will be stored in memory. The estimated future revisit time interval found in hypotheses 2 through 5 is modified in a last step by a reference memory for the amount of sugar water solution a bat gained at a feeder. This will result in shorter future revisit time intervals when the amount gained at this particular feeder is high and in longer revisit times when the amount received is low. This reference memory factor for the amount of sugar water is assumed to be time independent. Hypothesis 6 is similar to hypothesis 5, with an avoidance to visit the feeders that depends upon several past revisit time interval experiences. However, the estimated future revisit time interval is not modified by the reference memory for the amount gained at this feeder. All hypotheses with assumptions and parameters can be found in Table 5.1.

In the following we describe how the hypotheses were modelled in mathematical terms. The input to all models was restricted to four factors. The secretion rate at a particular feeder (sec_rate), the number of total visits in one night (n_t), the number of unrewarded visits (n_{unrew}), and the total sum of revisit times when no reward was received at a feeder (t_{unrew}). The models thus differed only in the way these factors were used for further computation.

Table 5.1: Overview of hypotheses and types of memory involved. For details see model description.

Hypothesis	***Memory for amount of nectar***	***Memory for time interval***
1	'rough' (see text)	no
2	Reference memory	Fixed time interval
3	Reference memory	Working memory for last revisit time interval
4	Reference memory	Working memory for time interval since last reward
5	Reference memory	Reference memory for last revisit interval
6	no	Reference memory for last revisit interval

The basic model (hypothesis 1) is patterned after a bat that will visit a feeder randomly and only adjusts its activity to the overall quality of a feeder. We modelled this with a poisson process, where the time until the first occurrence of a revisit is given by

$$t_{revist} = -\log_e(X^{(\frac{n_t}{720})}) \quad .$$

Here, X is a random variate drawn from the uniform distribution in the interval $0<X\leq1$. The exponent gives the rate or chance of occurrence of a revisit per minute (with 720 minutes per night = 12 h). In all models we computed n_t revisit times and calculated a distribution of the revisit times as done with the empirical revisit times.

In the following models we introduced an avoidance strategy for feeders that gave a reward recently. Thus, only the first visit after a reward had been obtained is calculated in a different manner from hypothesis 1. Once a bat has decided that it is profitable to visit a feeder again, it will visit the feeder in a fashion similar to hypothesis 1. Thus, beginning from the second visit after a reward, the visitation pattern is again modelled by a poisson process. The resulting revisitation pattern, to first avoid a feeder, and then, after a certain time interval has elapsed, visit this feeder with higher frequency, is modelled by following closely the break run break pattern observed in peak interval procedures (Gibbon 1977, Cheng & Westwood 1993).

The time interval for which the bats avoided a feeder after receiving a reward was generated from random Weibull-distributed variates. The Weibull distribution is used in engineering sciences for the assessment of the time duration until failure of a technical device. Instead of 'failure time' we used the 'time interval until revisit' as the corresponding parameter in the Weibull function. This revisit time interval was calculated as follows:

$$t_{revisit} = t_{goal} * -\log_e(X)^{\left(\frac{1}{(ref\ mem)}\right)} \quad .$$

Here, X is a random variate drawn from the uniform distribution in the interval $0<X\leq1$. The parameter ref_mem models the animal's estimate for the amount it has received at this feeder during previous visits. It is calculated and updated for each visit i as ref_mem(i)=(ref_mem(i-1) + amount of sugar water gained at visit i)/2. This gives an average of past and recent experiences. For hypothesis 6 the parameter ref_mem is held constant at 1.

The parameter t_{goal} represents the average time duration that a bat will avoid a feeder after having received a reward. For hypothesis 2 this parameter is held constant for all feeders, treatments and animals, and was set equal to the median of the empirical revisit time intervals for each animal on each day.

In the model for hypothesis 3, t_{goal} at visit i equalled the revisit time interval at visit i-1. For hypothesis 4, t_{goal} equalled the time interval since the last reward at this feeder. For hypothesis 5 we assumed a memory for multiple time intervals. In our model a bat could remember the last 20 time intervals (regardless of reward status). From the 20 revisit time intervals in memory we calculated the geometric mean as t_{goal}. This was done in accordance with results from the time bisection task, where it could be shown that temporal decisions of animals are based upon the geometric mean rather than the arithmetic mean of two time intervals (Church & Deluty 1977).

From hypotheses 2 through 6, the first visit after a reward is delayed such as described above. The following visits are again modelled by a poisson process. The revisit rate for this process is calculated from the empirical data as the quotient from the number of unrewarded visits and the sum of the empirical revisit interval times of these unrewarded visits: n_{unrew}/t_{unrew}. Thus, all other revisit time intervals following the first revisit after a reward are calculated as:

$$t_{revisit} = -\log_e(X)^{\left(\frac{n_{unrew}}{t_{unrew}}\right)} \quad .$$

For each hypothesis we calculated 10000 simulation runs for each animal for each phase and for each feeder containing n_t revisit time intervals if bats visited the feeder more than 50 times during that night. For each simulation run we then computed the distribution of the revisit time intervals by determining the proportion of visits per one minute interval. From the 10000 percentage values in each one minute interval we calculated the median and a 95 % confidence interval which equalled the 9750th and 250th highest proportion in an interval of one minute. We decided that we would not reject a hypothesis when less than 5 % of the empirical data could not be explained by the model. That is, when empirical data points were outside the boundaries of the 95 % confidence interval, the sum of the differences between the proportion of the data points and the nearest 95 % confidence interval should not exceed 0.05. For this we used only revisit intervals smaller than or equal 10 minutes. We chose the 5 % criterion as a conservative measure of how much of the variability that is inherent in the empirical data cannot to be explained by the model. The reasoning behind this is the fact that no model can give an exact picture of reality and some part of the variability in the empirical data remains unexplained. Thus, we decided for the 5 % criterion, while always bearing in mind that higher or lower values could lead to altered, if not entirely different results.

In some cases more than one hypothesis fit the results. We will thus present the results in two ways. We will first give the total proportion of cases that can be explained by a single hypothesis and then give the proportion of cases where this hypothesis fits as the most parsimonious one. The most parsimonious model is chosen in two steps. First, we determined the number of factors that enter a model. In the model for hypothesis 1, fewer factors are necessary than for hypotheses 2-6, because the number of unrewarded visits and the sum of unrewarded revisit time intervals is not included. Thus, the model of hypothesis 1 is the most parsimonious one. For hypothesis 2-6 we decided that keeping several time intervals in a reference memory is more complex than remembering just the last revisit interval, thus hypothesis 5 is more complex than hypothesis 3. We assumed the following complexity sequence for the hypotheses; 1<2<3<4<6<5.

Results

All bats found the feeders quickly during the training phase and visited the six feeders more or less regularly. In this study we investigated whether differences in revisit time intervals at a particular feeder depended upon the secretion rate. However, a change in revisit times could not only result from the underlying temporal reward scheme at each feeder, but also could result from the general activity of a bat. During the experimental nights, differences in revisit times to the feeders could be the result of differences in overall activity or total amount of nectar gained. A reduction in activity would lead automatically to longer revisit time intervals. However, there was no detectable difference in activity as it remained constant at 908 ± 505 visits per night (GLM (GEE):phase, day, phase*day: all Wald $\chi^2<1$; DF=1; all p>0.1). The high deviation can be explained by differences between animals, but there were no differences within animals. During experimental nights, bats visited all six feeders with the exception of animal 7, which visited only the top and lower row

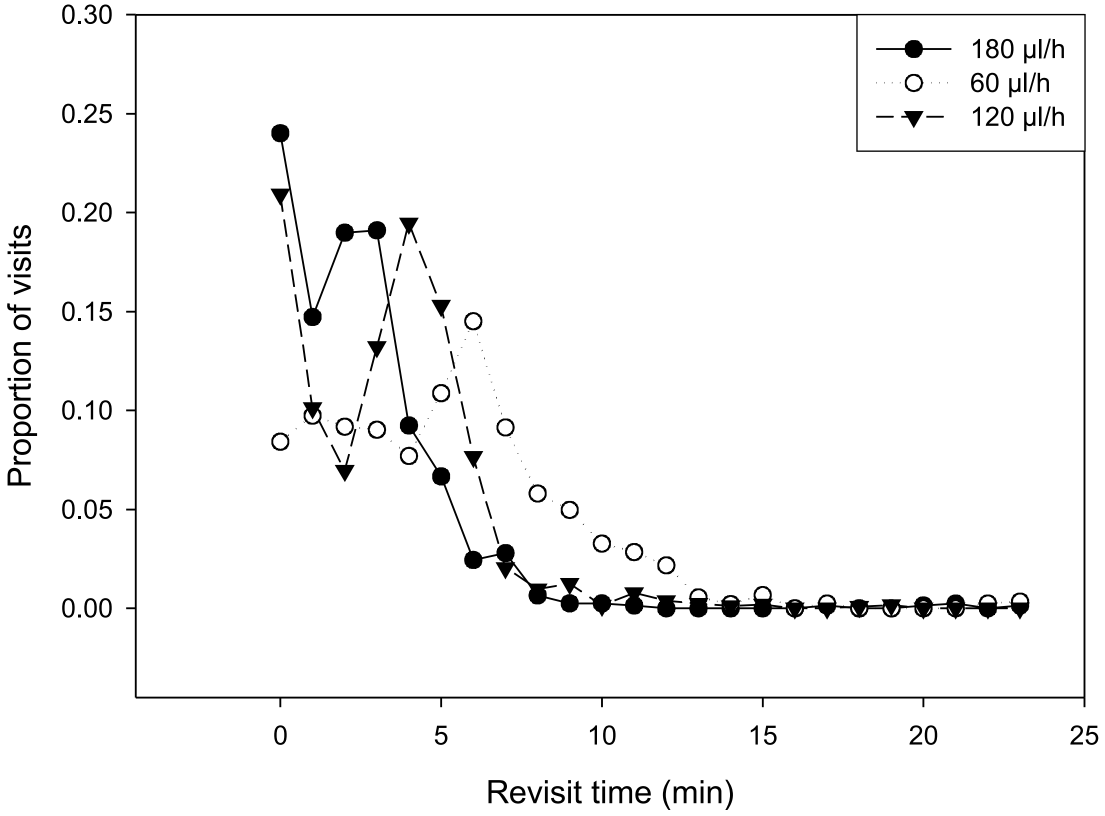

Figure 5.1: Distribution of revisit time intervals to all feeders on experimental day 2 and 4 of animal 1. Single graphs are given for the three treatment secretion rates of 60, 120, and 180 µl per hour. Ordinate shows proportion of total visits per condition, abscissa shows the revisit time interval at a single feeder in minutes.

feeders frequently and paid only occasional visits to the other two feeders of the middle row. A control of the experimental set-up revealed no apparent cause intrinsic to the system for this behaviour. The total amount of sugar water solution the bats received from the feeders amounted up to 7.9 ± 0.9 ml with no significant differences between the experimental conditions (GLM (GEE):phase, day, phase*day: all Wald $\chi^2<1.7$; DF=1; all p>0.1). Bats received 17.1 ± 5.7 µl per rewarded visit at the feeders. 424 ± 277.4 visits were unrewarded per night.

Reaction to different secretion rates

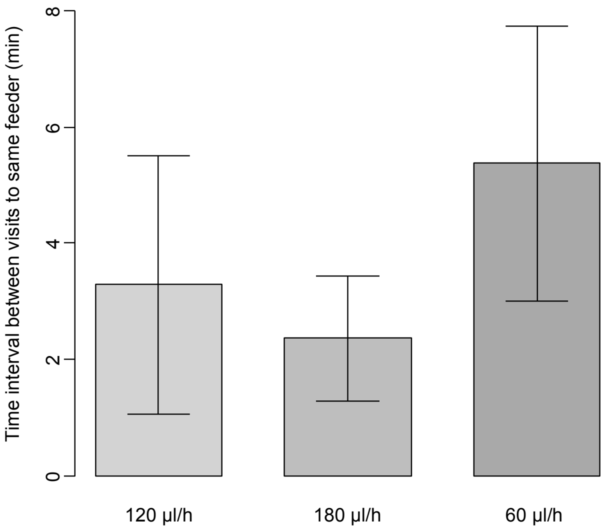

Figure 5.2: Median of revisit time intervals of all seven animals on the second day in the two experimental phases. Error bars show standard deviation. Abscissa shows the secretion rate in µl/h and ordinate shows the median of the revisit time intervals of the seven animals.

Bats showed clear reactions to the changing temporal reward pattern when comparing the second days of the two phases (for an example see Figure 5.1) A summary of the descriptive statistics of all animals and all feeders is given in Appendix A. With 120 µl per hour in phase 1, bats revisited a feeder after 3.2 ± 2.2 minutes. In phase 2 this time was increased to 5.37 ± 2.36 minutes at the low secretion rate feeders (60 µl per hour) and decreased to 2.4 ± 1.1 minutes at the high secretion rate feeders (180µl per hour) (Figure 5.2). The Cox proportional hazard model estimated a 1.9 times higher revisitation rate for low secretion rate feeders than for medium (120 µl/h) feeders (CoxPH: z=-5.13; p<0.01) and a 0.78 times lower revisitation rate (CoxPH: z=2.43; p<0.05) for high feeders in an overall significant model (robust score test=6.03; DF=2; p<0.05). If bats reacted to the two new feeder types in relation to the revisit times at the medium feeders, one would expect a change in revisitation rate of approximately 2 for the relation of medium to low secretion rate feeders (120 µl/ 60µl=2). And for the relation of medium to high feeders one would expect a value around 0.67 (120 µl/180 µl).

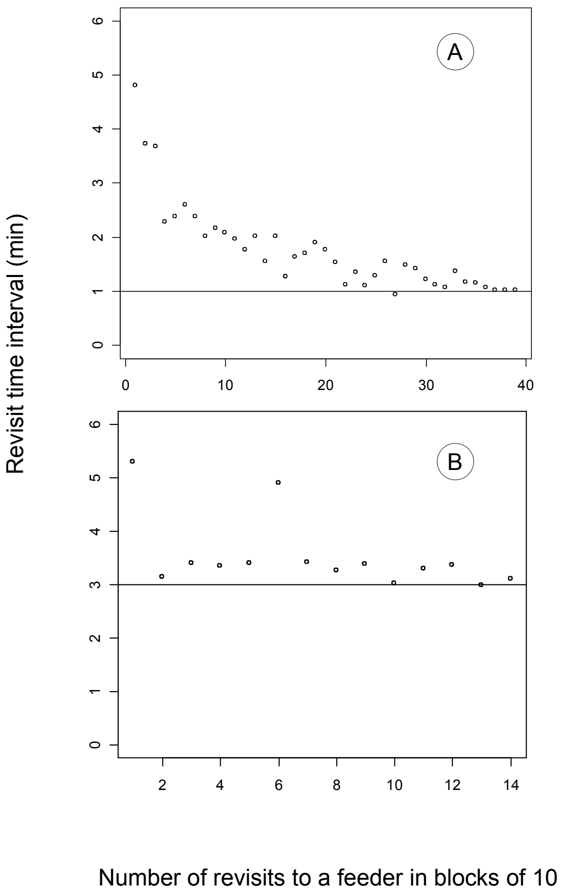

Figure 5.3: Learning of new secretion rate on day one in experimental phase two. Upper panel (A) shows development for high secretion rate feeders (180µl/h). Lower panel (B) shows the low secretion rate feeders (60µl/h). Both panels include seven animals, error bars have been omitted. Ordinate shows the median of the revisit time interval of the seven animals in minutes. Abscissa shows the progression of visits to single feeders in blocks of ten. Note that abscissa scale for A and B are different.

Learning after change of secretion rates

The first experimental night in phase 2 was the first experimental night when bats experienced feeders with different secretion rates. Here, we investigated how bats reacted to the changing temporal pattern. At both feeder types bats started at very similar values for the time intervals between visits of between 3 and 6 minutes during the first 30 visits. There was only a minor change of behaviour in reaction to the low secretion rate (Figure 5.3 b). The median of the revisit times adjusted very quickly to approximately 3 minutes, which equalled the time after which the low secretion rate feeders (60µl/h) first delivered a reward of 9 µl (Figure 5.3 b). The reaction to the high secretion rate feeders was much more pronounced as it declined after 400 visits to a feeder to approximately 1 minute, which also equalled the threshold when 9 µl were delivered (Figure 5.3 a). Thus, there was a detectable decline at both feeders that was dependent upon the experience of the animal (GLM (GEE); counter_10, Wald χ^2=43.9, DF=1, p<0.01). However, this decline was much stronger at high secretion rate feeders (counter_10*type, Wald χ^2=48.6, DF=1,p<0.01).

With the decline in revisiting time there was also a clear decrease in rewards per visit from 58.7 % rewards per visit in the low secretion rate feeders to a value below 10 %, and from 68.1 % to approximately 30 % in the high secretion feeders (GLM (GEE); counter_10, Wald χ^2=18.38, DF=1, p<0.01) The difference in rewards per visit between the two feeder types was highly significant (type, Wald χ^2=18.43, DF=1, p<0.01).

Results of theoretical model

The theoretical model was able to allocate 68% of the data to a specific hypothesis. However, the main part of distributions that could not be assigned to a specific hypothesis was caused by animal 6 (Table 5.2). This animal behaved entirely different from the other animals. This is not only founded on the inability to fit any theoretical model to the animal's data, but also to the high number of visits the animal made to the array. Animal 6 visited the feeders over 3600 times in two experimental nights which was nearly 4 times as often as all other animals did.

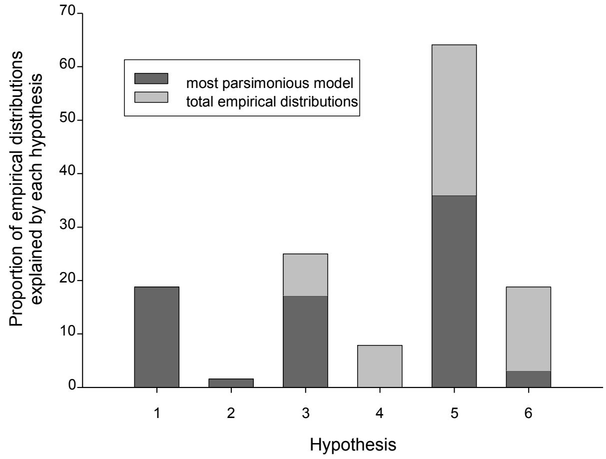

Figure 5.4: Fit of theoretical model to empirical data. Dark bars show proportion of empirical distributions of revisit time intervals that can be fitted by this model by the criterion to take the most parsimonious model (for details see model description). Light bars show the total proportion of empirical distributions that the model is able to be fit to. Ordinate shows the proportion of empirical distributions, abscissa shows the single models by hypothesis.

When animal 6 is excluded, there were 23.4% of visitation sequences to feeders that could not be explained by the theoretical model. The distributions of revisit interval times to feeders that could be explained were allotted to the different hypotheses as follows (excluding animal 6 and all feeding sequences at feeders with less than 50 visits): 18.8% hypothesis 1, 1.6% hypothesis 2, 17.2% hypothesis 3, 0% hypothesis 4, 35.9% hypothesis 5, and 3.1% hypothesis 6 (Figure 5.4, Table 5.2). Thus, revisit interval times could be explained mostly by hypotheses 1, 3, and 5. Examples of fitted models are given in Figure 5.5; all empirical distributions and the fitted theoretical distributions are given in Appendix B.

In the analysis above we looked at the most parsimonious model that fit the data. Another way to look at the fit of the data is to see how many distributions could have been explained by a single hypothesis regardless of whether a more parsimonious model existed. Here, we again applied the criterion that empirical data were allowed only to deviate by 5 % from the 95% confidence interval and excluded animal 6 and all sequences of visits to feeders containing fewer than 50 visits. In this case hypothesis 1 as the most parsimonious one was able to explain 18.8% of the empirical distributions of revisit time intervals. Hypothesis 2 was able to explain 1.6%, hypothesis 3: 25%, hypothesis 4: 7.9%, hypothesis 5: 64.1%, hypothesis 6: 18.8% (Figure 5.4).

Table 5.2: Fit of theoretical model to empirical data. For each animal and each phase the number of feeders that fit a hypothesis is given. No fit gives the number of feeders that can not be assigned to a specific hypothesis. Excluded are feeders that have been visited less than 50 times per experimental night.

Animal ID	***Phase***	***Hypothesis***						
		1	***2***	***3***	***4***	***5***	***6***	***No fit***
1	1	0	0	4	0	0	0	2
	2	2	0	2	0	1	0	1
2	1	3	0	2	0	1	0	0
	2	0	1	0	0	4	0	0
3	1	1	0	0	0	1	1	2
	2	2	0	0	0	3	1	0
4	1	0	0	0	0	5	0	1
	2	0	0	0	0	4	0	1
5	1	1	0	2	0	2	0	0
	2	3	0	0	0	2	0	1
6	1	0	0	0	0	0	0	6
	2	0	0	0	0	0	0	6
7	1	0	0	1	0	0	0	2
	2	0	0	0	0	1	0	3

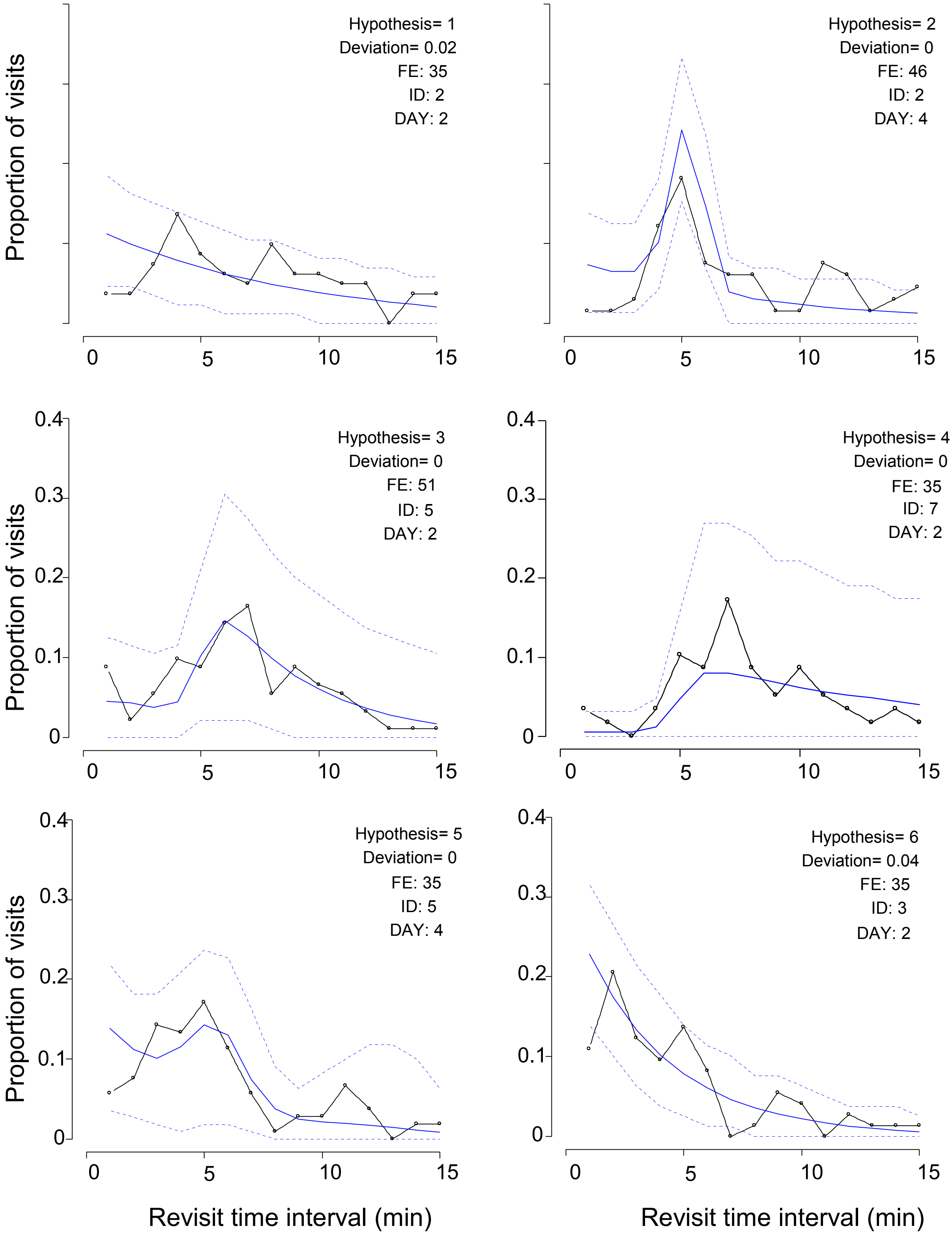

Figure 5.5: Examples for each hypothesis for an empirical distribution (black lines and circles) and the mean corresponding model (black line). The dashed line represents the 95% confidence interval around the mean of the model. The hypothesis, the animal id (ID), the experimental day (DAY), the feeder number (FE) and the the total deviation of the empirical model from the 95% confidence interval until 10 minutes is given in each panel. Ordinate shows proportion of total visits, abscissa shows the revisit time interval in minutes.

Discussion

In this study nectar-feeding bats were confronted with rewards of sugar water that changed in amount as a linear function of the time interval between two feeding visits. This reward schedule simulated the variable nectar availability at natural flowers where nectar secretion is a continuous process. Under natural conditions, bats will revisit single flowers many times a day at revisit intervals of less than an hour. We were interested to find out if bats that revisit the same flower many times use and are able to combine the information about revisit time interval and experienced reward magnitude to estimate nectar production rate. During our experiment with single bats at a set of six feeders, secretion rates were changed from a uniform rate at all six feeders to a low and a high rate at three feeders each. We investigated how bats reacted to these changing rates and analysed the behavioural patterns in order to deduce how bats used available information for future decisions.

First, bats changed their behaviour according to the secretion rate at a feeder such that they visited at shorter time intervals at feeders with an increased secretion rate and at longer time intervals at feeders with a decreased rate. This change did not result from an overall change in activity or from decreasing the total amount a bat gained per night. Instead, it was clearly a consequence of the underlying secretion rate at each feeder. Moreover, the reaction to different secretion rates followed neatly the relative increase respectively decrease in secretion rates, such that an increase in secretion rate resulted in a decrease of the revisit time interval at a feeder and that the amount gained per visit did not change. Thus, there seemed to be a mechanism that enabled bats to react to different secretion rates.

However, what information is perceived and integrated to solve the problem of returning too early to the feeders? The transitory behaviour of the bats after the change in secretion rate between experimental nights 2 and 3 suggests that at least some type of reference memory has to be involved. During the third experimental night bats adjusted their revisit behaviour to the new secretion pattern. This reaction was not an immediate change in behaviour as could be expected when only a working memory is involved (Cuthill 1994). Here, the change to adapt to increased secretion rate took between 150 and 400 visits to a single feeder. Although there was no immediate change at the low secretion rate feeders, we still conclude that some kind of reference memory has to be involved in the assessment of the secretion rate feeders and the according reaction.

Interestingly, the bats clearly discriminated between the low secretion rate and high secretion rate feeders very quickly as the revisit interval times at the low secretion rate feeders did not decrease like the revisit interval times at the high secretion rate feeders. This provides evidence that bats are able to discriminate between single flowers even on a small scale. This was accomplished most likely by a memory for several past experiences.

Theoretical model

The reference memory that seems to be involved in the decision-making process could involve two kinds of information; first, the amount gained at a visit, and second, the revisit time interval. Here, the theoretical models suggest that some of the observed data can easily be explained by a very simple mechanism, where the revisitation rate depends only on the total amount gained at a feeder. However, this simple cognitive mechanism can only account for a restricted part of the data. In some cases some animals employed a different strategy such that they adjusted their revisit time interval to a feeder in accordance to the last revisit interval and avoided a feeder for some time. This solution involves a working memory for the last revisit time interval at each feeder and a reference memory for the amount gained at this feeder. However, the main part of the empirical data can be explained only by a model in which animals possess a reference memory for revisit time intervals and for the amount of sugar water solution gained. Moreover, nearly two thirds of the empirical distributions of revisit intervals at a single feeder could be explained by hypothesis 5 (even though there were more parsimonious models). Cuthill and colleagues (1990, 1994) could show in European starlings (*Sturnus vulgaris*) that only the last time interval (a travel time) was used in the decision-making process that determined when to leave a patch. But they did not find a reference memory for time intervals. Thus, this seems to be evidence for the possible existence of a reference memory for time intervals. Moreover, this study provides the first evidence that bats are capable of integrating two types of information to estimate a production rate, the amount of nectar received and revisit time intervals at flowers.

However, not all bats responded equally well to the task in the experiment. Animal 6, e.g., visited extraordinarily often and we believe that it might not have been able to detect the underlying secretion rate. We designed the experiment such that bats would suffer from some mild food deprivation during experimental nights, but with regard to animal 6 we have to doubt that this constraint was severe enough. The behaviour of animal 7 supports the same line of argument. Animal 7 visited only 4 out of 6 feeders and thus received less sugar water solution than we had planned and was, nonetheless, in the same excellent shape as the other bats after the experiment.

This might also be the reason some animals (5,7) visited some feeders rather randomly and did not employ a more complicated strategy. However, the empirical data of animal 4, for example, and data at specific feeders for other animals could only be explained by a reference memory for both time intervals and amount of sugar water solution. Thus, we cannot conclude that every bat would employ a strategy involving reference memory for revisit time intervals under natural conditions. However, we have shown that a reaction to different secretion patterns is possible for a flower-visiting bat and that there is evidence that they are able to establish a reference memory for revisit time intervals to solve this problem even though not at all feeders.

The failure to detect a consistent pattern with all bats could not only originate from the lack of an energetic constraint but also from the neurologically expensive character to memorise several revisit time intervals for each feeder location. Here, we assume that memory will be associated with some cost so that a reference memory is more costly in terms of energy for building and maintaining the neurological tissue. However, we have to admit that evidence for these costs, although often postulated, is quite scarce (Dukas 2004, Mery & Kawecki 2004, Laughlin & Mendl 2004, Dukas 1999).

The model itself excluded (for simplicity reasons) physiological constraints that might account for some of the behavioural reactions the bats showed. We will not dispute that hunger and stomach contents as well as muscle fatigue might play an important role in deciding what to do next, especially in the natural environment. However, to our knowledge these physiological parameters can give no explanation for the avoidance of low secretion rate feeders when visiting a high secretion rate feeder that is just 0.4 m away. The mechanism for this behaviour has to be found on a cognitive level rather than a physiological one. Thus, it is possible that a part of the behaviour is guided by physiological processes that do not take place in the central nervous system, but the main part is surely under the control of cognitive processes.

Ecological implications

Does the use of a reference memory for the last revisit time interval, as in hypothesis 5, yield optimal results for the problem of how to visit a feeder that reproduces nectar over time? When bats in the theoretical model were assumed to possess only a memory for the time since the last reward (hypothesis 4), the theoretical distribution showed clear peaks at approximately 5 to 10 minutes minutes depending on the secretion rate. There were few visits where no reward was obtained at a feeder. This would, at least theoretically, lead to a higher amount of sugar water solution gained per visit. Again, one could reason that animals are not energetically limited in this experiment and thus can visit more often. However, in practice they employ a strategy that seems to involve a reference memory for revisit time intervals, which would not be necessary for a strategy that would orient by the time interval since the last reward at a feeder (hypothesis 4). So why is a reference memory for time intervals advantageous when foraging in natural environments; especially, when there is the possibility that simpler strategies would result in similar energetic gain while requiring less neurological architecture?

In natural environments flower-visiting bats encounter more than six flowers. They may visit more than 50 different flowers per night (Winter & von Helversen 2001). This experiment provides no evidence that bats will follow the secretion pattern of each flower closely. However, it is likely that bats will assess the secretion rate and calculate the optimal point in time when to return, at least for flowers with high secretion rates or high energetic gain. For this, all revisit time intervals should be taken into account since zero or nearly zero rewards can surely occur. By taking each revisit time interval into account it would be possible to react more flexibly upon changes than to remember only the intervals since the last reward. Moreover, bats could calculate the earliest point in time when a revisit is energetically rewarding by integrating the energetic gain with costs for return. Coming too late will bring the risk of being too late since some other bat may have already visited this flower. The optimisation problem flower visiting bats have to solve in a natural environment is a trade off between waiting long enough for the nectar to build up and visiting early enough to beat other competitors to this particular flower (see also Bateson 2003). Flower visiting-bats seem to have adapted to this difficult task by developing cognitive abilities that make use of the at least partial predictability of their environment.

Literature

Baker, H. G., Baker, I., and Hodges, S. A. (1998). Sugar composition of nectars and fruits consumed by birds and bats in the tropics and subtropics. *Biotropica, 30,* 559-586.

Basil, J. A., Kamil, A. C., Balda, R. P., and Fite, K. V. (1996). Differences in hippocampal volume among food storing corvids. *Brain Behavior and Evolution, 47,* 156-164.

Briggs, C. J. and Hoopes, M. F. (2004). Stabilizing effects in spatial parasitoid-host and predator-prey models: a review. *Theoretical Population Biology, 65,* 299-315.

Brodbeck, D. R. (1994). Memory for Spatial and Local Cues - A Comparison of A Storing and A Nonstoring Species. *Animal Learning & Behavior, 22,* 119-133.

Carthew, S. M. and Goldingay, R. L. (1997). Non-flying mammals as pollinators. *Trends in Ecology & Evolution, 12,* 104-108.

Cheng, K. and Westwood, R. (1993). Analysis of Single Trials in Pigeons Timing Performance. *Journal of Experimental Psychology-Animal Behavior Processes, 19,* 56-67.

Church, R. M. and Deluty, M. Z. (1977). Bisection of Temporal Intervals. *Journal of Experimental Psychology-Animal Behavior Processes, 3,* 216-228.

Clark, T. G., Bradburn, M. J., Love, S. B., and Altman, D. G. (2003). Survival analysis part IV: Further concepts and methods in survival analysis. *British Journal of Cancer, 89,* 781-786.

Crawley, M. J. (2002). Statistical Computing: An Introduction to Data Analysis using S-Plus. New York: John Wiley and Sons Ltd.

Cuthill, I. C., Haccou, P., and Kacelnik, A. (1994). Starlings (Sturnus-Vulgaris) Exploiting Patches - Response to Long-Term Changes in Travel-Time. *Behavioral Ecology, 5,* 81-90.

Cuthill, I. C., Kacelnik, A., Krebs, J. R., Haccou, P., and Iwasa, Y. (1990). Starlings Exploiting Patches - the Effect of Recent Experience on Foraging Decisions. *Animal Behaviour, 40,* 625-640.

Dobat, K. and Peikert-Holle, T. (1985). Blüten und Fledermäuse (Chiropterophilie). Frankfurt: Kramer Verlag.

Fortin, D. (2002). Optimal searching behaviour: the value of sampling information. *Ecological Modelling, 153,* 279-290.

Gibbon, J. (1977). Scalar Expectancy-Theory and Webers Law in Animal Timing. *Psychological Review, 84,* 279-325.

Healy, S. D. and Hurly, T. A. (2004). Spatial learning and memory in birds. *Brain Behavior and Evolution, 63,* 211-220.

Healy, S. D. and Krebs, J. R. (1996). Food storing and the hippocampus in Paridae. *Brain Behavior and Evolution, 47,* 195-199.

Hirvonen, H., Ranta, E., Rita, H., and Peuhkuri, N. (1999). Significance of memory properties in prey choice decisions. *Ecological Modelling, 115,* 177-189.

Huber, R., vanStaaden, M. J., Kaufman, L. S., and Liem, K. F. (1997). Microhabitat use, trophic patterns, and the evolution of brain structure in African cichlids. *Brain Behavior and Evolution, 50,* 167-182.

Iwasa, Y., Higashi, M., and Yamamura, N. (1981). Prey Distribution As A Factor Determining the Choice of Optimal

Foraging Strategy. *American Naturalist, 117,* 710-723.

Jaeger, R. G., Barnard, D. E., and Joseph, R. G. (1982). Foraging Tactics of A Terrestrial Salamander - Assessing Prey Density. *American Naturalist, 119,* 885-890.

Janson, C. H. (1998). Experimental evidence for spatial memory in foraging wild capuchin monkeys, Cebus apella. *Animal Behaviour, 55,* 1229-1243.

Kamil, A. C. (1978). Systematic Foraging by A Nectar-Feeding Bird, Amakihi (Loxops-Virens). *Journal of Comparative and Physiological Psychology, 92,* 388-396.

Krebs, J. R., Clayton, N. S., Healy, S. D., Cristol, D. A., Patel, S. N., and Jolliffe, A. R. (1996). The ecology of the avian brain: Food-storing memory and the hippocampus. *Ibis, 138,* 34-46.

Krebs, J. R. and Inman, A. J. (1992). Learning and Foraging - Individuals, Groups, and Populations. *American Naturalist, 140,* S63-S84.

Lefebvre, L., Nicolakakis, N., and Boire, D. (2002). Tools and brains in birds. *Behaviour, 139,* 939-973.

Lemke, T. O. (1984). Foraging Ecology of the Long-Nosed Bat, Glossophaga-Soricina, with Respect to Resource Availability. *Ecology, 65,* 538-548.

Ohashi, K. and Thomson, J. D. (2005). Efficient harvesting of renewing resources. *Behavioral Ecology, 16,* 592-605.

Pacini, E., Nepi, M., and Vesprini, J. L. (2003). Nectar biodiversity: a short review. *Plant Systematics and Evolution, 238,* 7-21.

Paton, D. C. and Carpenter, F. L. (1984). Peripheral Foraging by Territorial Rufous Hummingbirds - Defense by Exploitation. *Ecology, 65,* 1808-1819.

Shettleworth, S. J. (1998). Cognition, Evolution, and Behavior. New York: Oxford University Press.

Shettleworth, S. J. and Plowright, C. M. S. (1992). How Pigeons Estimate Rates of Prey Encounter. *Journal of Experimental Psychology-Animal Behavior Processes, 18,* 219-235.

Todd, P. M. and Gigerenzer, G. (2000). Precis of Simple heuristics that make us smart. *Behavioral and Brain Sciences, 23,* 727-+.

Watts, D. P. (1998). Long-term habitat use by mountain gorillas (Gorilla gorilla beringei). 2. Reuse of foraging areas in relation to resource abundance, quality, and depletion. *International Journal of Primatology, 19,* 681-702.

Winter, Y. (1999). Flight speed and body mass of nectar-feeding bats (Glossophaginae) during foraging. *Journal of Experimental Biology, 202,* 1917-1930.

Winter, Y. and Stich, K. P. (2005). Foraging in a complex naturalistic environment: capacity of spatial working memory in flower bats. *Journal of Experimental Biology, 208,* 539-548.

Winter, Y. and von Helversen, O. (2001). Bats as Pollinators: foraging energetics and floral adaptations. Pages 148-170 *in* L. Chittka and Thomson, J.D. eds. Cognitive ecology of pollination. Cambridge University Press, Cambridge.

Chapter 6

Risk sensitivity to food amounts in nectar-feeding bats: a behavioural mechanism for the ideal free distribution

Abstract

Scalar expectancy theory predicts risk averseness for animals that are confronted with a choice between constant and variable options with respect to the amount of food received. We tested this hypothesis in a natural foraging paradigm with bats of the nectar-feeding species *Glossophaga commissarisi*. The bats maintained in a group showed a clear preference for the constant option and thus behaved according to theory. These results contrast previous observations of bats maintained individually that behaved indifferent to variability in amount. This behaviour difference between group-living and individually kept animals may be explained by a new hypothesis of the adaptive value of risk sensitivity presented here. It is suggested that variability serves nectar-feeding animals as an indicator for the degree of exploitation competition encountered at a resource. Thus, a reaction to variability might be the behavioural mechanism that leads to an ideal free distribution of a population within the resource space.

Introduction

NUMEROUS STUDIES HAVE shown that animals are risk- averse to variability in amounts and risk prone to variability in delays of food rewards (Kacelnik and Bateson 1996). More precisely, this means that animals which are given the choice between two resources that are equivalent in their energy content but differ in the variability of this content will choose the constant alternative if the amount of food is varied. By contrast, if the delay in obtaining food is varied after a signal has announced upcoming food delivery animals opt for the variable option.

Choice preferences between equicaloric options are not predicted by simple normative models based on optimal foraging theory. An animal that is confronted with two food resources should opt for the alternative that will maximize its energy intake. Only under the assumption of a more sophisticated interaction between energy state, chance of survival and probabilities of finding little or much food can normative models based on reasoning about fitness consequences of choices explain why the choice for constant food amount or variable food delay options might increase fitness (McNamara and Houston 1992).

The energy budget rule, as the most prominent (Stephens 1981), assumes a non-linear utility function of energy intake dependent on energy state. It predicts animals to be risk-prone in energetically desperate situations, where even the slim possibility of a large gain may be the only chance of survival. On the other hand, animals should not push their luck and thus be risk-averse or risk-insensitive on a balanced energy budget.

On a different level, process-based explanations do not consider the potentially adaptive value of risk sensitive behaviour. The scalar expectancy theory extends Weber's law to processes of memory. It states that the preference for a risky or non- risky option is mediated by the combination of a perceptional and memory retrieval bias which can be explained by the Weber-Fechner law (Kacelnik and Abreu 1998).

Empirical studies examining risk sensitivity of animals to variability in amounts of food have produced conflicting results in different species. Several of them can be accounted for by neither putative fitness benefits, according to the energy budget hypothesis, nor do they fit in the scheme of scalar expectancy theory (see Bateson 2002 for a review). In some cases no risk sensitivity or even risk-prone behaviour to amounts has been detected even though the animals acted on a balanced energy budget (Kacelnik and Bateson 1996). As pointed out by Bateson (2002), no theory today is consistent with all phenomena associated with risk-sensitivity. This shortcoming of present theories may lie in their negligence of relevant but unknown parameters that stem from the specific ecological conditions under which an animal species has evolved and is confronted with in nature. Thus knowledge of the behaviour of a taxonomically and ecologically broader range of animal species may be necessary to further refine the theory. Especially the taxonomic and ecological diversity within mammals has so far been largely neglected, as the majority of studies within mammals have been based on rodents such as rats and mice.

Here, we present the first study of risk sensitivity in a nectarivorous mammal. Bats of the species *Glossophaga commissarisi* were tested in a naturally designed foraging paradigm for their risk-sensitivity to amounts of nectar. The dominant mode of intraspecific competition for nectar in this species is based on exploitation rather than interference competition (Tschapka 1993). This leads us to a new explanation of the phenomenon of risk-sensitivity by linking it to the mechanisms underlying the ideal free distribution.

Materials and Methods

This study was conducted in the lowland Atlantic rainforest of Costa Rica at La Selva Biological Station. Two nights prior to the experiment we caught six bats (two females, four males) of the common (Tschapka 2004) species *Glossophaga commissarisi* with mist-nets, and caged these animals together in an experimental shade house (4 x 6 2.35 m) with a solid roof erected within the forest, isolated from station disturbances. The bats were tested under their natural light regime, with dusk at approximately 18:00 h and dawn at 06:00 h. During day-time animals rested together in a small basket that hung from the ceiling in a small sheltered compartment of the shade house, and showed no observable agonistic interactions with each other. All bats received necklaces with RFID transponders (150 mg) for real-time, automatic individual identification at experimental feeders. Average nightly temperatures and humidity differed only slightly (22 ± 1 °C; >90% rel. humidity. La Selva OTS Meteorological Station). After completion of the experiments all bats were released at the site of capture.

Six computer-controlled sugar water feeders hung from the shade house ceiling 1.8 m above ground. The bats fed while hovering, licking the sugar solution from the base of a feeder. Visits were detected and timed by a computer interrogated photo electric sensor and bats could be rewarded with a predefined amount of sugar solution (17% w/w) by opening an electronic valve. Individuals during hovering were identified in real-time (less than 80 ms) and with a reliability of >99% by a transponder reader installed at each feeder and connected to the computer.

We accustomed bats to the experimental surroundings and the feeders by offering constant amounts of 50 µl of sugar water solution for each visit to a feeder for two nights. Already during the first night all six bats used each of the six feeders frequently and were thus trained successfully to the experimental set-up.

After a bat had visited a feeder this was deactivated for 10 s to prevent continuous revisits. Due to real-time individual identification, this software-controlled deactivation was specific to those individuals that had visited recently.

The experimental manipulation took place in the third and fourth nights. In the third night, half of the six feeders delivered constant amounts of 50 µl per visit while the other half gave variable amounts of either 100 µl or 0 µl, with a 50% probability of each (later referred to as positions A). This resulted in constant and variable feeders with equal mean amounts (50 µl) of sugar solution given. Nectar amounts were within the natural uptake capability of the bats (Winter, unpublished data).

In the fourth night the constant and variable conditions were reversed for each feeder (positions B). This manipulation was necessary to control for spatial preferences of the bats and so to exclude the possibility that the choice for a certain feeder was influenced by its spatial position and not by variation in the amount of food received.

As pointed out by Kacelnik and Bateson (1996), handling time is an important experimental variable that needs to be controlled between treatments. A shorter handling time could cause a preference for one type of feeder due to energetic advantages. Here handling time accorded to the amount of time bats spent hovering in front of a feeder. It was measured from the signal from the photoelectric sensor at each feeder.

The data from this experiment were the automatically collected events of individually identified visits (to feeders differing in variation of nectar amount) by six individual bats kept together in a group. For the statistical analysis we transformed proportional data of individual choice with an arcsine transformation and then tested against random choice with a t-test (Univariate procedure SAS Institute 1999-2001). For a comparison of hovering durations we used a repeated measures generalized linear model (Genmod procedure SAS Institute 1999-2001) with a link function according to a gamma distribution. χ^2 and P values refer to likelihood ratios test of

Proc Genmod.

Results

All six bats visited the feeders frequently. Each animal visited the feeders between 80 and up to 370 times per night. The activity remained constant with an average of 215.3 (±SD = 69.0) visits per animal during the first, and 193.5 (±SD = 136.8) visits during the second experimental night. From this, each individual bat received between 6 and 18 ml sugar water solution per night, which is enough to balance the energy budget of differently active individuals (Winter and von Helversen 2001).

Bats hovered in front of feeders for average durations of 739 (±SD = 406) ms in the first night and 612 (±SD = 479) ms in the second. Thus there was no detectable difference in handling times between the two experimental positions A and B ($\chi^2 = 0.38$; df = 1; $P = .54$) nor between the constant and variable feeder types ($\chi^2 = 0.03$; df = 1; $P = .86$) or the interaction between both ($\chi^2 = 3.05$; df = 1; $P = .08$; $N = 2,453$). This analysis was conducted by taking into account each single hovering duration.

Bats were kept together as a group and ‘high traffic’ in front of preferred feeders could potentially have influenced feeder choice. However, overall activity in front of feeders was very low. Taken together, the total hovering duration of all bats summed to 15.9 minutes in night 1 and 11.9 minutes in night 2. Hence bats spent less than 1% of the experimental time in front of the feeders.

In both spatial arrangements of feeders the bats preferred the constant (91.9% and 76.1%) over the variable (9.1% and 23.9%) feeders with a significant deviation from random choice (Fig. 1; pos A: $t = 17.02$, $P < .001$; pos B: $t = 3.18$, $P < .05$; $N= 6$). The preference for constant feeders at positions A was much stronger than at positions B (Fig. 1). In addition there was also a higher between individual variance at positions B (see Fig. 1). This can be explained by the following observations: i. Bats had to adopt to the change in the constant/variable regime between feeders and needed about 50 to 100 initial visits before they flew to the constant feeders with regularity. It proved difficult to find a criterion that would consistently eliminate this sampling phase for all bats so we included the whole data set in the analysis. We are aware that risk can only be estimated if mean and variation of a reward rate are already known to the subjects. However, we obtained a statistically significant effect even when we included this phase of uncertainty in the analysis. ii.

After approximately 200 visits two individuals showed a transitory preference for the variable feeders (nearly 100 %) but changed back to constant rewards after visiting about 40 times. These two individuals were also those that consumed overall the largest amount of nectar during the night. iii. One animal showed nearly random choice between constant and variable feeders (but had been consistent in preference for constant feeders during positions A treatment).

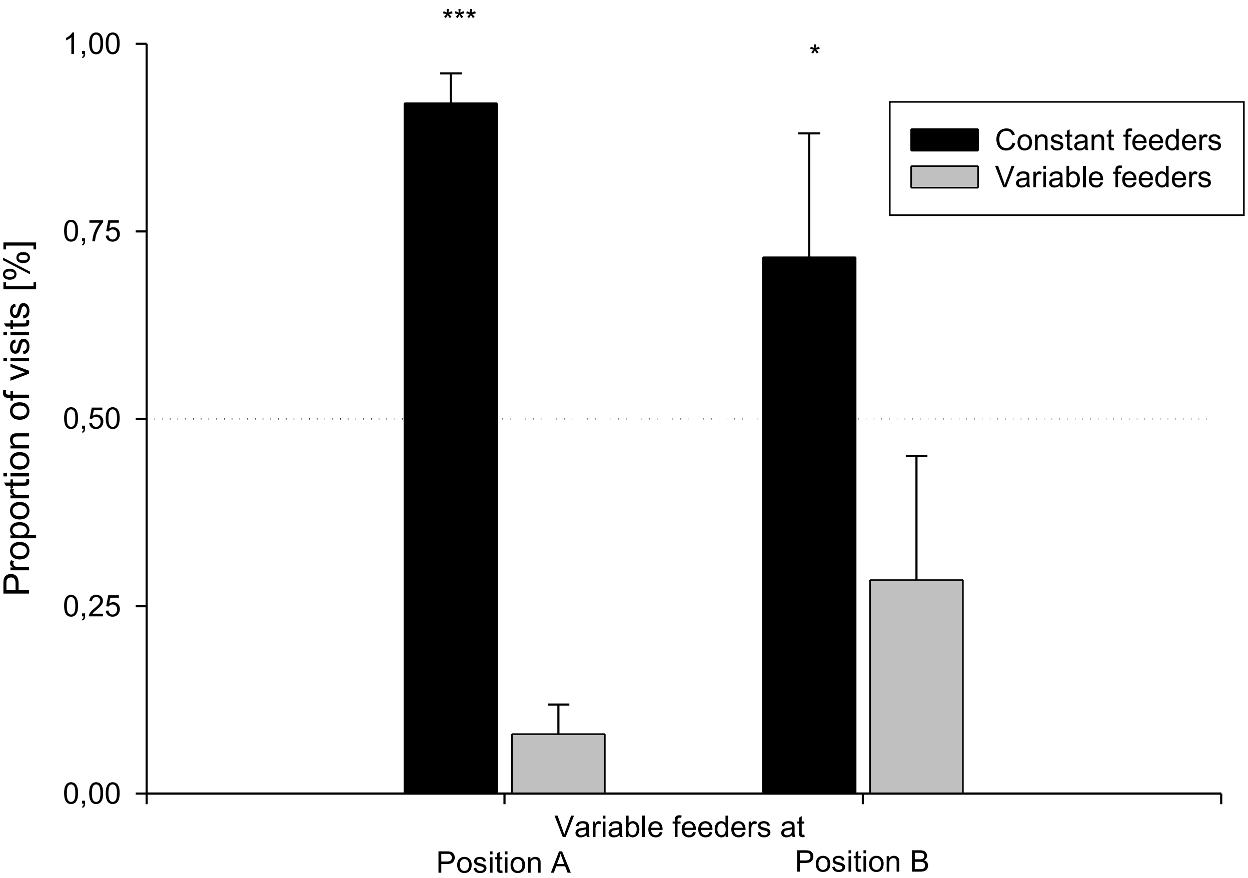

Figure 6.1: Mean proportion of choices for constant or variable feeders presented at reversed spatial positions during two experimental conditions. Proportion of variable choices tested against random choice (dotted line). Constant feeders gave 50 µl rewards and variable feeders 100 µl or 0 µl with equal probability. Error bars show the standard deviation of overall mean calculated from individual means. Data from six bats based on n=1291 (positions A) and n=1161 (positions B) choices. Bats were first presented with variable feeders at positions A.

Discussion

The results from this experiment are straightforward. The bats showed a clear preference for those artificial flowers that gave constant amounts of sugar water. This behaviour was independent of spatial feeder arrangement because it was maintained even after reward regimes had been switched between feeder positions. There was no difference in handling times between the constant and variable reward options, measured here as hovering duration. Thus we can exclude the possibility that handling effort biased the decision process. We can also exclude that a lack of sampling led to a bias for the constant option since bats explored all flowers at the beginning of the night. The results are compliant with scalar expectancy theory in showing risk-averseness to variability in amount.

Compliance of experimental results with process-based scalar expectancy theory does not require further evolutionary arguments as the behavioural bias might simply be a non-adaptive consequence of the underlying Weber's-law-compliant neural mechanism an animal cannot escape. Nonetheless one may still explore the possibility of adaptive value. Why should a nectar-feeding bat not use all resources equally but instead strikingly prefer constant flowers?

Here, we propose a new hypothesis concerning the adaptive value of risk sensitivity. When flower-visiting bats forage in a natural environment they encounter numerous flowers and patches of flowers with different qualities. Flowers are not likely to move and nectar is replenished over time. *Glossophaga* bats are able to remember and revisit flowers that provided them with nectar (Thiele and Winter 2004; Stich and Winter, unpublished data). As these bats do not form territories but have overlapping activity areas (Winter and von Helversen 2001; Thiele and Winter, unpublished data) all individuals of a population are potentially exposed to exploitation competition at flowers. This could be a main reason for variability in amounts of food available at a food location with constant renewal rate. If two or more bats exploit the same flower for nectar it may result in a discrepancy between the expected and experienced amount of food. Even if bats did not have a time memory, they could still learn that visits during regular and repetitive foraging routines normally lead to constant returns. The deviation from an expected value could be taken as an indicator for the activity of other individuals and the strength of competition at this particular flower. If confronted with the option between a flower with relatively constant rewards over regular time intervals (no competition) and a variable flower (competition) even with equal energetic content an animal should for reasons outlined below mainly choose constant flowers as long as they are available.

Shafir (2000) showed in a meta-analysis that the choice of an animal for the constant or variable volume option is closely correlated with the coefficient of variation (CV = s.d./mean). He showed that a high coefficient of variation in the variable option results in a decrease of choices for this option if animals act risk-aversely. This dependence of behaviour on the coefficient of variation means that for the same absolute value of standard deviation animals still differ in their choices when means differ. In terms of the hypothesis presented here it would mean that high competition (high standard deviation) is tolerable as long as the mean gain from the food source is high so that the CV is kept low. On the other hand, if the competition at a particular flower is too high an animal might opt for another less visited flower even though the high competition flower has an equal energy content.

A prediction derived from our hypothesis of competition driven risk-sensitivity is that any type of variability that does not depend on competition should have a much smaller effect on the behaviour of animals. Such indifferent behaviour is actually seen in experiments that manipulated the concentration rather than the amount of nectar. Nectar concentration is a consequence of a plant's secretory mechanisms and is not influenced by nectar consumers. Bananaquits, *Coereba flaveola*, (Wunderle and Obrian 1985) and some social hymenopterans (Waddington 1995; Fulop and Menzel 2000) react indifferently to variations in nectar concentration, or at least react much less than to variations in nectar amount. Variability in nectar concentration carries no information about competition. On the other hand, animals for which the dominant mode of intraspecific competition is not based on exploitation but on interference should be less reactive to variability in nectar amount. Territorial rufous hummingbirds, *Selasphorus rufus*, for example react more strongly to variability in nectar concentration than to variability in nectar amount (Bateson et. al., unpublished data). Territoriality is based on interference competition and thereby avoids exploitation competition (but see also Lucas and Waser 1989). Thus flower parameters which contain information about the degree of exploitation competition should be of lesser importance and so not influence the choice behaviour of territorial animals.

These findings are compliant with our hypothesis of risk-sensitivity as a mechanism to avoid competitors. But why should there be an adaptive value to the evaluation of competition? And what is the function of avoiding competition even though the energy intake at two food sources is equal?

A long standing concept in foraging ecology is the ideal free distribution (Fretwell and Lucas 1970, Sutherland 1996). It states that food patches with low competition should be preferred over patches with high competition in respect of their profitability. The behavioural reaction at an individual level to competition will lead to a distribution where all individuals of a population are able to maximize their intake rate. This distribution is called 'ideal free', in the sense that individuals of a population distribute ideally over the available resources. 'Free' relates to the assumption that no energetic and spatial constraints hinder individuals. However, a prerequisite of the ideal free distribution is a competitor which must possess some means of measuring the degree of competition at a local resource. This is often accomplished by observing con-specifics. Yet if direct interaction between individuals takes place only rarely other mechanisms should have evolved to ensure the detection of competition. The sensitivity to variability could constitute such a mechanism.

In our experiment the competition at the variable feeders was seemingly high, with a coefficient of variation of 100, and the competition at the constant feeders was low. Thus apart from being compliant with scalar expectancy theory the choice for the constant feeder could be interpreted as a choice for the low competition option. The bats were certainly aware of the other competitors in our experimental setting and the unusually strong reaction to variability could be caused by perception of the continuous presence of conspecifics in the immediate vicinity.

Garrison and Gass (1999) found that a traplining hummingbird, *Phaethornis longirostris*, reacted to an artificial competition situation by visiting those feeders more often at which they encountered increased variance that was experimentally caused through simulated competition. Thus hummingbirds showed a behaviour that might be interpreted as being risk-prone. However, after a period of time when the hummingbirds experienced no effect of their increased exploitation behaviour on the reward schedule, they avoided the variable feeders. The results of earlier and preliminary experiments with *Glossophaga* bats fit this line of reasoning (Winter, unpublished data) where risk averseness to amounts of sugar water could not be detected. One important difference between this earlier and the present experiment was that in previous experiments bats were tested singly, while in the present study all six individuals were kept together in a group and foraged simultaneously in one flight cage.

The data gathered in this experiment cannot suffice to fully support our hypothesis. But we made concrete prediction for what we expect in future experiments. Thus, these thoughts can serve as an incentive for designing more experiments and models that incorporate the interaction between individual cognitive abilities, the resulting individual decision and the implications for dynamics on population level.

Literature

Bateson, M. 2002. Recent advances in our understanding of risk-sensitive foraging preferences. Proceedings of the Nutrition Society 61:1-8.

Fretwell, S. D. and H. J. Lucas. 1970. On territorial behavior and other factors influencing habitat selection. Acta Biotheoretica 19:16-36.

Fulop, A. and R. Menzel. 2000. Risk-indifferent foraging behaviour in honeybees. Animal Behaviour 60:657-666.

Garrison, J. S. E. and C. L. Gass. 1999. Response of a traplining hummingbird to changes in nectar availability. Behavioral Ecology 10:714-725.

Kacelnik, A. and F. B. E. Abreu. 1998. Risky choice and Weber's law. Journal of Theoretical Biology 194:289-298.

Kacelnik, A. and M. Bateson. 1996. Risky theories - the effects of variance on foraging decisions. American Zoologist 36:402-434.

Lucas, J. R. and P. M. Waser. 1989. Defense through exploitation - a skinner box for tropical rain forests. Trends in Ecology & Evolution 4:62-63.

McNamara, J. M. and A. I. Houston. 1992. risk-sensitive foraging - a review of the theory. Bulletin of Mathematical Biology 54:355-378.

Shafir, S. 2000. Risk-sensitive foraging: the effect of relative variability. Oikos 88:663-669.

Stephens, D. W. 1981. The logic of risk-sensitive foraging preferences. Animal Behaviour 29:628-629.

Sutherland, W. J. 1996. From individual behaviour to population ecology. Oxford University Press, Oxford.

Sutherland, W. J. and G. A. Parker. 1992. The relationship between continuous input and interference models of ideal free distributions with unequal competitors. Animal Behaviour 44:345-355.

Tschapka, M. 2004. Energy density patterns of nectar resources permit coexistence within a guild of neotropical flower-visiting bats. Journal of Zoology 263:7-21.

Waddington, K. D. 1995. Bumblebees do not respond to variance in nectar concentration. Ethology 101:33-38.

Winter, Y. and von Helversen, O. 2001. Bats as pollinators: foraging energetics and floral adaptations. Pages 148-170 *in* L. Chittka and Thomson, J.D. eds. Cognitive ecology of pollination. Cambridge University Press, Cambridge.

Wunderle, J. M. and T. G. Obrien. 1985. Risk-aversion in hand-reared bananaquits. Behavioral Ecology and Sociobiology 17:371-380.

Chapter 7

General Discussion

THIS THESIS WAS focused on the question what cognitive abilities will enable a nectar-feeding bat, *Glossophaga soricina*, to efficiently forage on floral nectar, a resource that is spatio-temporally predictable. Moreover, how do they relocate a particular, previously visited flower and how do they decide at what point in time they should return?

With regard to the relocation of a flower, Winter and Stich (2005) could already show that bats are able to remember particular locations and return to them. In this thesis, I could additionally show that bats do not solely rely on global cues or cues given by the flower itself (petals, corolla) to relocate an inflorescence, but that cues that are near (40 - 80 cm) the goal can have an impact when relocating a goal (chapter 2). Thus, bats possess the ability to form stimulus goal associations even though the spatial contiguity is not given. This is even more surprising when keeping in mind that experiments took place in total darkness and that bats were not able to perceive the experimental arena as a whole. The ability to form associations across a distance is also found in nectarivorous rufous hummingbirds (Brown &Gass 1993, Brown 1994), but not in humans (Iwai 1986). This cognitive ability, although of subordinate importance in the relocation process, seems to be a specialised adaptation that is especially helpful for nectar-feeding animals when distinguishing between individual flowers that look alike.

But even when returning to the correct flower, a bat has to estimate the point in time when it is profitable to return to this particular flower. For this estimation, bats need to assess two informations at a visit; first, how much nectar did they receive and second, how much time has elapsed since the last visit. First, I investigated these two parameters separately. I could show that bats are indeed able to distinguish between different volumes of sugar water solution (chapter 3) and thus are capable to estimate how much nectar they received at a visit. Moreover, bats can also time small intervals as they react maximally after a reinforced time interval in a modified fixed interval schedule, the peak procedure (chapter 4).

However, these two abilities alone are not representing specialised adaptations to the foraging ecology of a flower-visiting bat. The ability to discriminate between different volumes, although seldom tested, seems to be a rather universal ability. And also the ability to time small intervals has been tested and detected in a number of species (Cheng & Roberts 1991, Brodbeck et al. 1998, Rodriguez-Girones & Kacelnik 1999, Rakitin et al. 1998).

However, can bats also employ this information in a natural context? Can they perceive different rates at different flowers and base their revisit decisions on this information? In a paradigm where bats encountered feeders with three different secretion rates, bats reacted to the underlying pattern so that they avoided feeders with lower secretion rate for a longer time interval than feeders with a higher secretion rate (chapter 5). There was clear evidence that this is a clear reaction to the simulated secretion rate and not only to the amount bats received at individual feeders. More surprisingly, I found evidence from a priori models that bats remember and use several earlier experienced items of the available information at a flower visit. This means that bats seem to possess a reference memory for several time intervals and several amounts of sugar water solution for each individual feeder.

Mechanisms of timing

The computational models from chapter 5 that simulate a bat, which forages on a renewable resource, give important insights into the mechanism of how timing in the seconds to minutes interval could work. Until now, pacemaker models, like the scalar expectancy theory (SET), have been used to explain the timing behaviour of animals, especially with regard to empirical data from the peak procedure (Gibbon 1977, Malapani & Fairhurst 2002). These models have not been without criticism. They were able to explain a good portion of timing data. However, the neurological basis for a pacemaker and especially the accumulator for the pulses of the pacemaker could not be detected until now. Thus, the possibility of a pacemaker free model is explored (Staddon & Higa 1999, Staddon et al. 2002, Staddon 2005). Here, memory dynamics constitute the main part of the mechanism of interval timing. When experiencing a reward, the memory of this experience decays with increasing time. Once the memory strength for the last experience falls below a threshold that is associated with this particular location or event, the animal starts to react again. In my models I incorporated such a pacemaker free timing in the simulation of the bats. The amount of nectar, bats received at a visit to a feeder, influenced the speed of the decay process. The time interval that has elapsed can be understood as the rest of the memory strength associated with the prior event, which influences the threshold. However, the models showed that it was not sufficient to explain the empirical data that only the most recent experience at the feeder influenced the decision to return to the feeder. For a good portion of the data, the model fitted the empirical data only when including a reference memory that would integrate several past experiences.

This memory decay model is more parsimonious than the SET as no pacemaker or accumulator is required. Only well known processes like memory decay, reference memory, and associative learning are required. Although the model cannot account for all of the empirical data, the study described in chapter 5 might point the way for future research in the investigation of timing in animals.

Cognition and ecology

In the beginning of this study stood the question of how the ecology of an animal would influence not only the morphological traits but also the more hidden cognitive abilities of an animal. And here, in one of the first examples, we could show that the estimation of an rate is possible for an animal. This has large-scale consequences.

There are only few studies that tackle the problem of if and how a rate can be estimated by an animal (Shettleworth & Plowright 1992, Jaeger et al. 1982 , Cuthill et al. 1990, Cuthill et al. 1994). Here, a rate is defined as the number of items or the amount of a resource that is encountered or picked up in a certain time interval. Even very basic models of foraging are based on the assumption that animals somehow possess this cognitive ability. Animals base their decision when to leave a patch on the encounter rate with prey or, as in the case of flower-visiting bats, have to decide when to return to a renewable resource (Bateson 2003). And although, in some cases, purely physiological, non-neuronal processes like digestion or hunger might account for the decisions of animals, there is little doubt that also cognitive processes are involved. The present study shows for the first time that an animal possesses the ability to estimate rates from several past experiences and that the decision-making process is based on this information.

Flower-visiting bats show this ability in a very prominent form as they are not only able to estimate the rate at one single flower, but bats in the experiment from chapter 5 were able to employ the information from several feeders and react accordingly. Thus, bats possess, additional to their excellent spatial memory (Winter & Stich 2005, Thiele &Winter 2005), the ability to associate informations about the quality of a flower with each single flower location. The quantity of places that can be memorised in such a way was not explored in study.

Thus, bats seem to have developed an excellent memory for the location and quality of flowers, but what are the implications when leaving the laboratory surroundings and looking at bats in their natural environment. Which scenarios can be found?

In a very simple scenario, there would be only one bat and one flower. It gets more complicated, if one bat and several flowers are involved. The last, most likely scenario is computationally demanding since here several bats forage on multiple flowers. This is where another factor becomes important; exploitation competition. A flowers quality is now not only determined by the underlying secretion rate, but also by the variability caused by the bats themselves.

Thus, I explored the possibility that bats could react to a given variability and thus try to avoid competition at particular flowers (chapter 6). If returning to a flower, a bat has an expectation of how much nectar should be available at this flower since it has estimated the production rate at this flower. If the expectation is not met, there could be some competitor that also exploits this flower. When estimating the competitional pressure via the variability of a resource, individual bats will either exclude the flower from their foraging bouts when the competition is too high or will still visit this flower when the competition is still endurable. By this mechanism, a population of bats could distribute over the standing crop in ideal free manner (Sutherland 1996).

Admittedly, there is not much data supporting this hypothesis, but it is a good starting point to search for the adaptive value of the found rate estimating mechanism, which seems not to be the neurologically simplest solution for foraging on flowers, under the assumption that a bat is alone. Thus, I assume that the adaptive value for this mechanism has to lie in the advantage that it becomes possible to foretell how the dynamics in a spatio-temporally predictable environment will develop even in the presence of competitors.

Perspectives for future studies

In this study, I could only add one more piece to the complex puzzle that makes up the foraging behaviour of flower-visiting bats. Many interesting points remain and future research should be directed at three main issues.

First, the mechanistic aspect of interval timing. More evidence is needed to explore the possibility that the ability to time intervals is not based upon a pacemaker, but can also be explained by memory decay processes. Models like that of Staddon (2005) and the one presented in this study can generate explicit predictions about the timing behaviour of animals in different paradigms. Especially the administration of drugs that influence memory processes can help distinguish between a pacemaker and a pacemaker free mechanism.

Second, there are still open questions regarding the impact of the cognitive abilities on the behaviour in natural environments. Controlled experiments with multiple individuals that experience exploitation competition and field studies will reveal more of the dynamics behind the decision-making process of these bats while foraging.

Third, there is the possibility to adapt the paradigm from chapter 4 to other species like mice, rats, pigeons, or hummingbirds. This comparative approach could provide further insights into the different mechanisms in the species and if the pronounced ability of flower-visiting bats to estimate nectar production rates is a special case, or if this ability is common throughout the animal kingdom.

Literature

Bateson, M. (2003). Interval timing and optimal foraging.

Brodbeck, D. R., Hampton, R. R., and Cheng, K. (1998). Timing behaviour of black-capped chickadees (Parus atricapillus). *Behavioural Processes, 44,* 183-195.

Brown, G. S. (1994). Spatial Association Learning by Rufous Hummingbirds (Selasphorus-Rufus) - Effects of Relative Spacing Among Stimuli. *Journal of Comparative Psychology, 108,* 29-35.

Brown, G. S. and Gass, C. L. (1993). Spatial Association Learning by Hummingbirds. *Animal Behaviour, 46,* 487-497.

Cheng, K. and Roberts, W. A. (1991). 3 Psychophysical Principles of Timing in Pigeons. *Learning and Motivation, 22,* 112-128.

Cuthill, I. C., Haccou, P., and Kacelnik, A. (1994). Starlings (Sturnus-Vulgaris) Exploiting Patches - Response to Long-Term Changes in Travel-Time. *Behavioral Ecology, 5,* 81-90.

Cuthill, I. C., Kacelnik, A., Krebs, J. R., Haccou, P., and Iwasa, Y. (1990). Starlings Exploiting Patches - the Effect of Recent Experience on Foraging Decisions. *Animal Behaviour, 40,* 625-640.

Gibbon, J. (1977). Scalar Expectancy-Theory and Webers Law in Animal Timing. *Psychological Review, 84,* 279-325.

Iwai, E., Yaginuma, S., and Mishkin, M. (1986). Acquisition of Discrimination-Learning of Patterns Identical in Configuration in Macaques (Macaca-Mulatta and Macaca-Fuscata). *Journal of Comparative Psychology, 100,* 30-36.

Jaeger, R. G., Barnard, D. E., and Joseph, R. G. (1982). Foraging Tactics of A Terrestrial Salamander - Assessing Prey Density. *American Naturalist, 119,* 885-890.

Malapani, C. and Fairhurst, S. (2002). Scalar timing in animals and humans. *Learning and Motivation, 33,* 156-176.

Rakitin, B. C., Gibbon, J., Penney, T. B., Malapani, C., Hinton, S. C., and Meck, W. H. (1998). Scalar expectancy theory and peak-interval timing in humans. *Journal of Experimental Psychology-Animal Behavior Processes, 24,* 15-33.

Rodriguez-Girones, M. A. and Kacelnik, A. (1999). Behavioral adjustment to modifications in the temporal parameters of the environment. *Behavioural Processes, 45,* 173-191.

Shettleworth, S. J. and Plowright, C. M. S. (1992). How Pigeons Estimate Rates of Prey Encounter. *Journal of Experimental Psychology-Animal Behavior Processes, 18,* 219-235.

Staddon, J. E. R. (2005). Interval timing: memory, not a clock. *Trends in Cognitive Sciences, 9,* 312-314.

Staddon, J. E. R., Chelaru, I. M., and Higa, J. J. (2002). Habituation, memory and the brain: the dynamics of interval timing. *Behavioural Processes, 57,* 71-88.

Staddon, J. E. R. and Higa, J. J. (1999). Time and memory: Towards a pacemaker-free theory of interval timing. *Journal of the Experimental Analysis of Behavior, 71,* 215-251.

Sutherland, W. J. (1996). From individual behaviour to population ecology. Oxford: Oxford University Press.

Thiele, J. and Winter, Y. (2005). Hierarchical strategy for relocating food targets in flower bats: spatial memory versus cue-directed search. *Animal Behaviour, 69,* 315-327.

Winter, Y. and Stich, K. P. (2005). Foraging in a complex naturalistic environment: capacity of spatial working memory in flower bats. *Journal of Experimental Biology, 208,* 539-548.

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Appendices

Appendix A: Summary table of experimental results from chapter 5. Revisit times at feeders for individual animals

Appendix B: Figures give all distributions of revisit time intervals of all individual animals with computational model of the most parsimonious hypothesis that fitted the empirical data. Figures are just like Figure 5.5 with descriptions: Hypothesis = most parsimonious model, ID= Animal number; Deviation= Sum of deviation of empirical data from model; FE= Feeder number, Day=experimental day (day 2= all feeders 120 µl/h; day 4= three feeders 60 µl/h, three feeders 180 µl/h)

Appendix C: File list of raw data and analysis files included on the CD-ROM in this thesis

Appendix A

Animal id number	experimental day	feeder number	secretion rate	total visits	non rewarded visits	sum revisit time interval of non rewarded visits	mean revisit time interval	standard deviation revisit time interval	median revisit time interval	median adjusted deviation revisit time interval
1	2	35	120	174	53	123.70	4.37	2.73	4.65	2.05
1	2	37	120	161	42	115.26	4.79	2.42	4.70	1.50
1	2	42	120	199	73	176.71	3.78	2.47	4.03	2.56
1	2	46	120	213	86	136.11	3.61	2.62	3.69	2.66
1	2	51	120	244	114	175.05	3.12	2.56	2.91	2.82
1	2	53	120	253	125	185.46	2.99	2.76	2.73	2.98
2	2	35	120	86	20	120.43	8.59	6.44	7.40	5.48
2	2	37	120	85	17	86.46	8.78	7.49	6.59	3.97
2	2	42	120	65	8	73.65	11.31	8.96	9.21	6.25
2	2	46	120	60	14	135.62	11.82	13.66	7.91	6.77
2	2	51	120	65	6	57.11	10.86	7.18	8.92	4.68
2	2	53	120	101	22	98.00	7.07	5.07	6.08	4.46
3	2	35	120	79	31	126.31	8.54	14.05	3.93	3.54
3	2	37	120	58	18	117.28	11.51	21.10	4.55	3.55
3	2	42	120	81	36	217.38	8.23	15.48	3.45	2.93
3	2	46	120	86	37	172.02	8.06	13.87	3.35	2.88
3	2	51	120	83	40	202.17	8.58	15.37	2.66	2.31
3	2	53	120	100	54	223.30	6.64	17.98	2.34	2.40
4	2	35	120	172	76	232.14	4.05	5.62	3.22	1.30
4	2	37	120	331	234	387.01	2.51	4.67	1.69	1.37
4	2	42	120	181	91	256.47	3.51	2.45	3.18	1.57

Appendix A

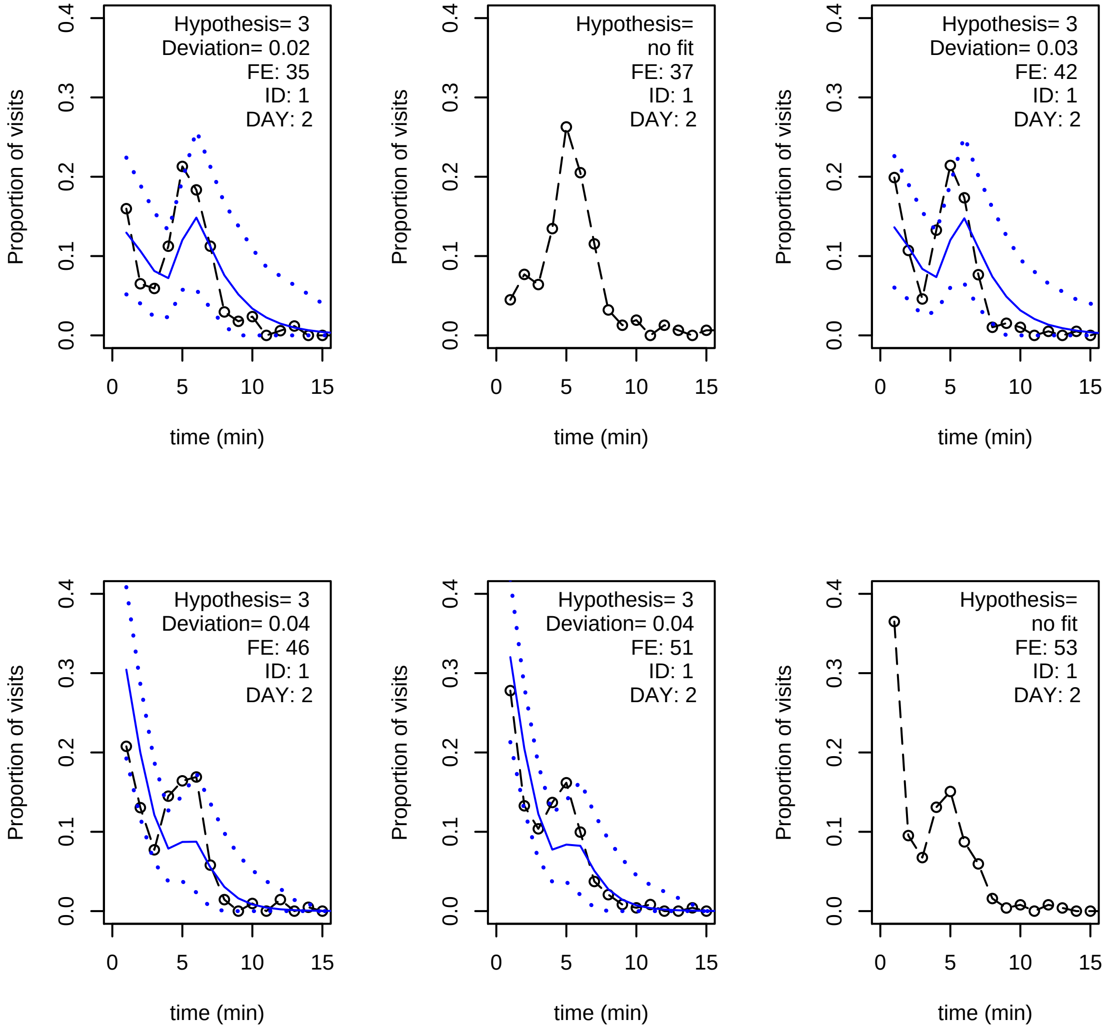
Animal id number	experimental day	feeder number	secretion rate	total visits	non rewarded visits	sum revisit time interval of non rewarded visits	mean revisit time interval	standard deviation revisit time interval	median revisit time interval	median adjusted deviation revisit time interval
4	2	46	120	157	78	240.42	3.67	3.52	2.91	1.40
4	2	51	120	325	216	389.60	2.03	1.99	1.66	0.96
4	2	53	120	362	245	399.29	2.06	4.78	1.40	0.92
5	2	35	120	78	6	46.88	7.89	4.19	7.04	2.38
5	2	37	120	75	15	85.68	9.49	6.91	7.93	3.96
5	2	42	120	49	11	67.48	7.98	4.54	7.36	4.21
5	2	46	120	80	17	150.27	8.84	8.96	7.13	3.74
5	2	51	120	95	22	90.13	7.22	7.29	6.13	3.27
5	2	53	120	145	59	296.96	4.78	4.15	3.86	3.49
6	2	35	120	373	248	445.82	1.84	0.92	1.69	0.85
6	2	37	120	316	197	415.34	2.17	0.85	1.99	0.70
6	2	42	120	428	305	516.94	1.64	0.95	1.50	0.91
6	2	46	120	380	258	881.02	1.98	1.02	1.83	0.66
6	2	51	120	307	186	394.72	2.24	0.98	2.11	0.94
6	2	53	120	364	239	435.90	1.89	0.86	1.72	0.67
7	2	35	120	63	20	217.35	11.52	9.18	7.98	4.58
7	2	37	120	170	87	351.28	4.36	7.03	1.75	1.29
7	2	42	120	7	3	45.38	21.81	24.14	11.48	15.50
7	2	46	120	11	6	790.78	60.86	106.40	11.31	15.61
7	2	51	120	40	13	210.49	17.27	17.13	11.66	12.67
7	2	53	120	293	202	444.98	2.64	5.73	0.80	0.68

Appendix A

Animal id number	experimental day	feeder number	secretion rate	total visits	non rewarded visits	sum revisit time interval of non rewarded visits	mean revisit time interval	standard deviation revisit time interval	median revisit time interval	median adjusted deviation revisit time interval
1	4	35	60	100	40	193.59	7.47	4.66	6.88	2.97
1	4	37	180	229	70	105.75	3.34	3.07	3.01	2.10
1	4	42	180	231	74	140.39	3.27	3.02	3.00	1.95
1	4	46	60	139	77	239.68	5.45	4.74	4.78	3.93
1	4	51	60	155	88	250.31	4.91	3.93	4.67	3.41
1	4	53	180	319	150	189.79	2.38	2.64	1.78	1.65
2	4	35	60	48	8	105.67	14.95	9.32	12.24	6.35
2	4	37	180	134	25	80.72	5.47	3.84	4.46	2.51
2	4	42	180	150	48	146.98	4.81	4.21	3.41	2.58
2	4	46	60	72	30	242.47	10.75	11.24	7.06	5.13
2	4	51	60	74	31	200.79	10.10	8.71	7.63	5.82
2	4	53	180	206	76	236.96	3.51	2.78	2.70	1.72
3	4	35	60	62	17	159.43	11.17	6.42	9.74	5.92
3	4	37	180	164	51	144.63	4.30	3.84	3.12	2.48
3	4	42	180	154	45	146.66	4.63	4.25	3.25	2.06
3	4	46	60	72	30	230.99	9.22	7.32	6.67	4.41
3	4	51	60	63	22	251.65	10.97	10.71	8.43	5.17
3	4	53	180	260	136	195.36	2.92	4.26	1.35	1.34
4	4	35	60	108	51	276.47	6.24	2.86	5.61	1.87
4	4	37	180	232	92	217.65	2.96	1.90	2.59	0.93
4	4	42	180	185	61	168.31	3.53	2.77	2.83	1.31

Appendix A

Animal id number	**experimental day**	**feeder number**	**secretion rate**	**total visits**	**non rewarded visits**	**sum revisit time interval of non rewarded visits**	**mean revisit time interval**	**standard deviation revisit time interval**	**median revisit time interval**	**median adjusted deviation revisit time interval**
4	4	46	60	42	9	154.77	16.42	16.31	12.94	7.61
4	4	51	60	167	103	382.58	4.16	2.52	3.58	1.37
4	4	53	180	569	394	462.57	1.45	3.25	0.90	0.56
5	4	35	60	110	59	241.14	6.62	7.92	4.46	3.09
5	4	37	180	161	62	187.17	4.53	6.55	2.81	2.27
5	4	42	180	71	14	244.37	10.34	22.30	6.04	4.69
5	4	46	60	76	31	203.57	9.68	8.96	8.42	5.06
5	4	51	60	65	26	257.80	11.07	16.41	5.71	3.72
5	4	53	180	218	105	239.55	3.34	5.67	1.81	1.59
6	4	35	60	163	105	371.31	4.36	5.73	3.38	1.67
6	4	37	180	289	152	328.04	2.49	4.46	1.74	0.94
6	4	42	180	329	183	469.69	2.26	3.96	1.69	1.16
6	4	46	60	187	126	469.51	3.96	5.38	3.29	1.64
6	4	51	60	151	92	1118.86	4.74	5.89	4.02	1.81
6	4	53	180	333	209	1120.93	2.09	4.12	1.47	1.00
7	4	35	60	93	34	227.44	7.96	8.65	4.04	2.70
7	4	37	180	120	56	271.79	6.29	7.79	2.89	2.27
7	4	42	180	0	0	0.00	0.00	0.00	0.00	0.00
7	4	46	60	3	2	128.43	123.96	6.31	123.96	6.62
7	4	51	60	85	47	337.55	8.90	13.29	3.81	2.56
7	4	53	180	221	135	341.00	3.44	6.08	1.10	0.84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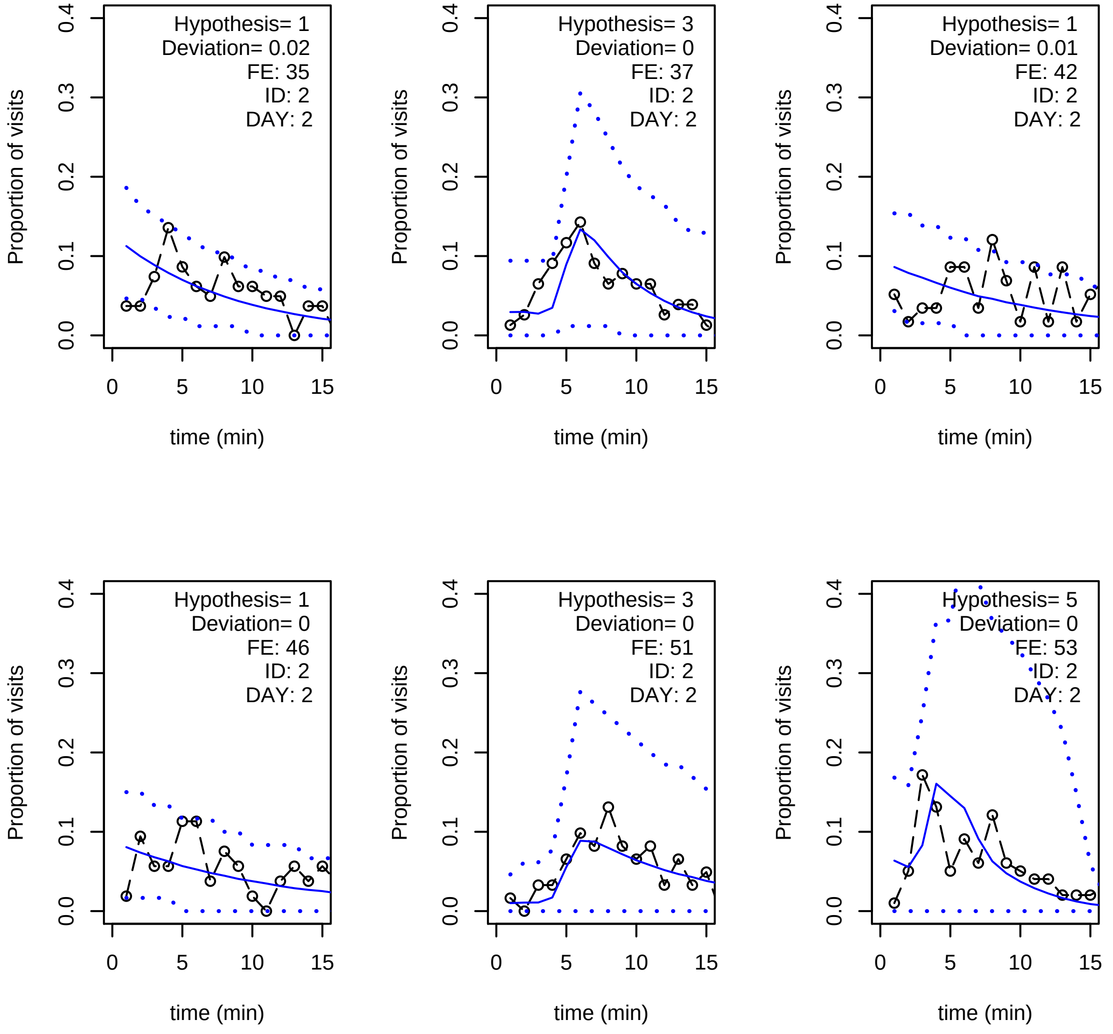
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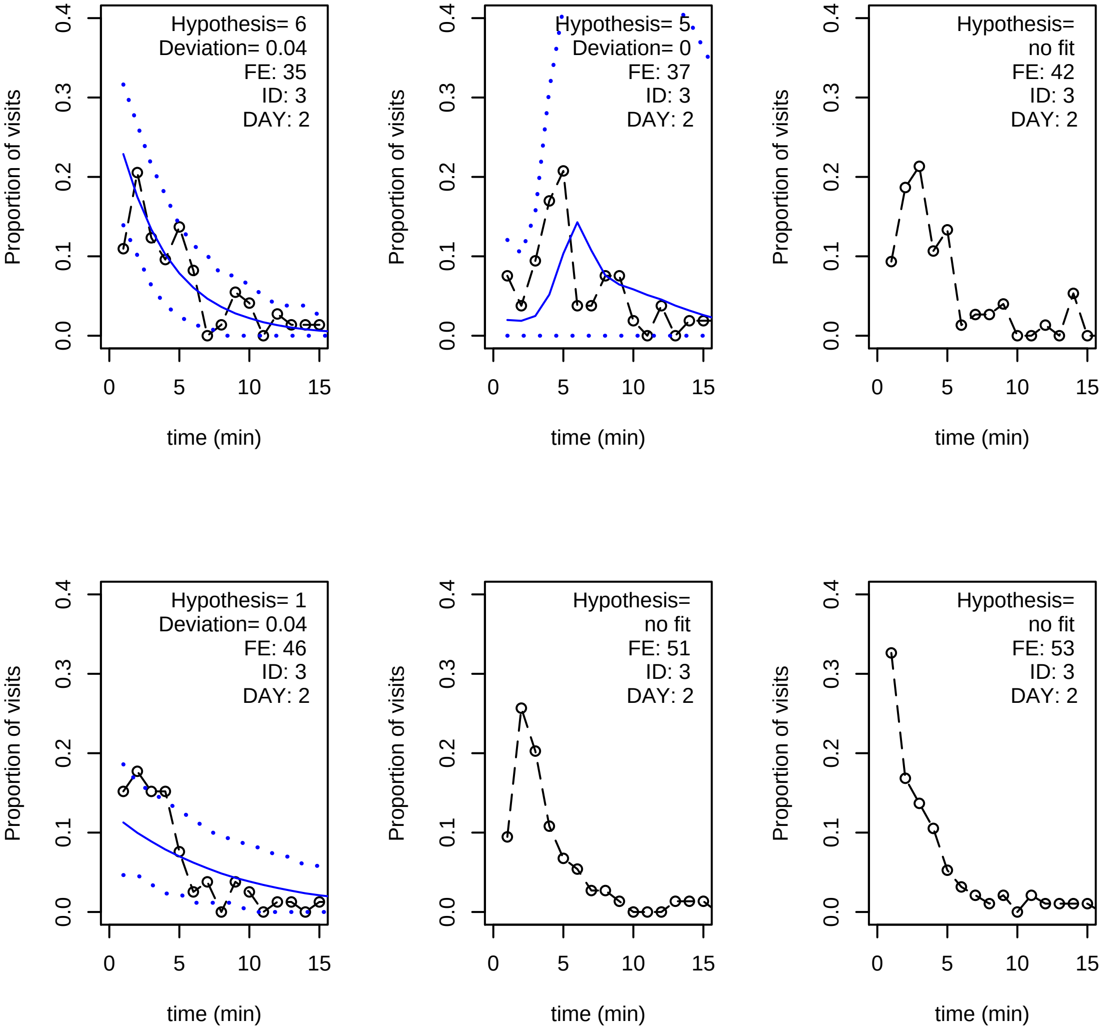
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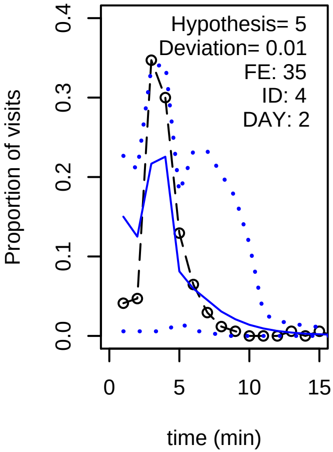
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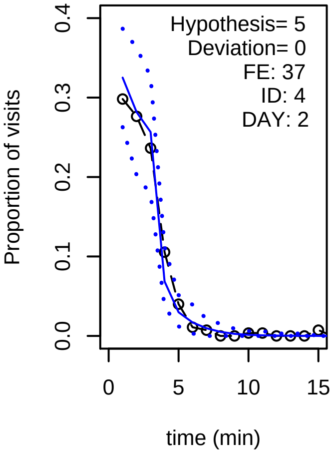
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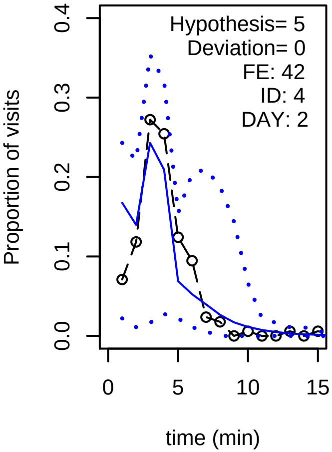
5
10
15
time (min)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Deviation= 0
FE: 42
ID: 4
DAY: 2
Proportion of visits
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0.1
0.2
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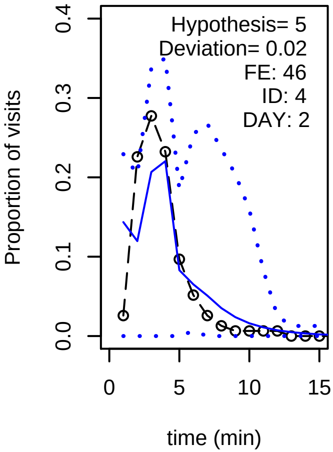
0.4
0
5
10
15
time (min)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Deviation= 0.02
FE: 46
ID: 4
DAY: 2
Proportion of visits
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0.4
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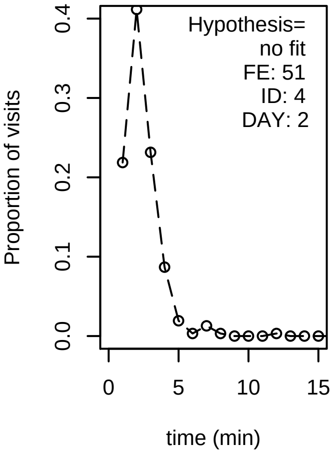
time (min)


Hypothesis=
no fit
FE: 51
ID: 4
DAY: 2
Proportion of visits
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0.1
0.2
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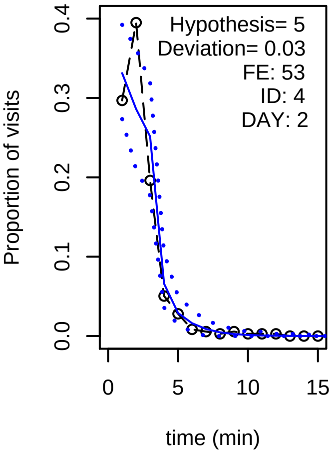
0.4
0
5
10
15
time (min)


Hypothesis= 5
Deviation= 0.03
FE: 53
ID: 4
DAY: 2
Proportion of visits
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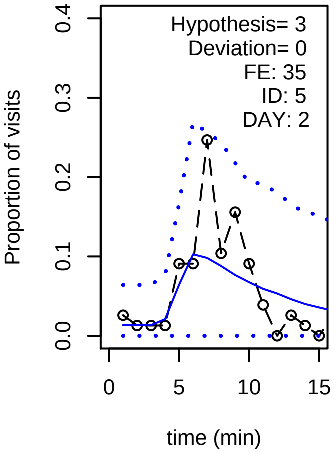
0.1
0.2
0.3
0.4
0
5
10
15
time (min)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Deviation= 0
FE: 35
ID: 5
DAY: 2
Proportion of visits
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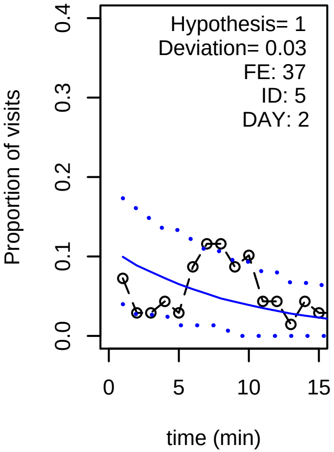
0.1
0.2
0.3
0.4
0
5
10
15
time (min)


Hypothesis= 1
Deviation= 0.03
FE: 37
ID: 5
DAY: 2
Proportion of visits
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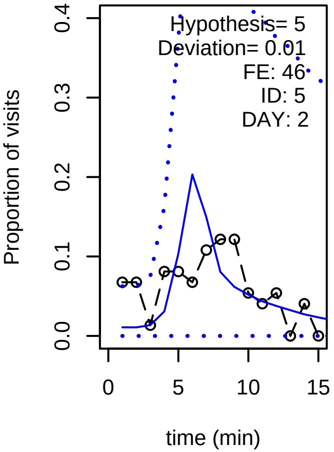
0.1
0.2
0.3
0.4
0
5
10
15
time (min)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Deviation= 0.01
FE: 46
ID: 5
DAY: 2
Proportion of visits
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0.2
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0.4
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10
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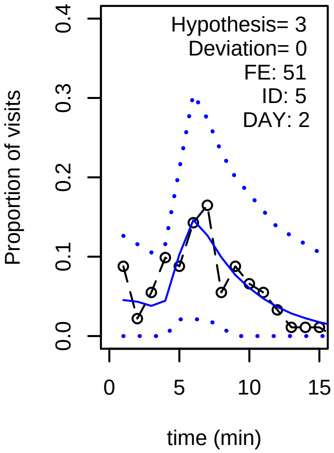
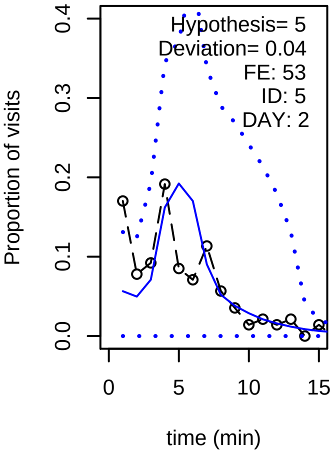
time (min)


Hypothesis= 3
Deviation= 0
FE: 51
ID: 5
DAY: 2
Proportion of visits
0.0
0.1
0.2
0.3
0.4
0
5
10
15
time (min)


Hypothesis= 5
Deviation= 0.04
FE: 53
ID: 5
DAY: 2
Proportion of visits
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0.4
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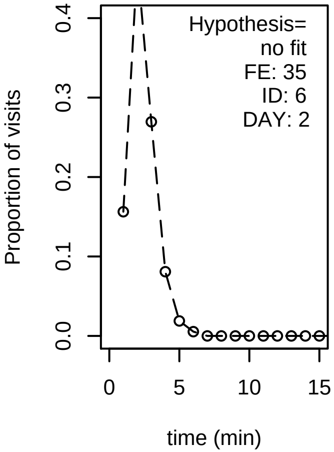
time (min)


Hypothesis=
no fit
FE: 35
ID: 6
DAY: 2
Proportion of visits
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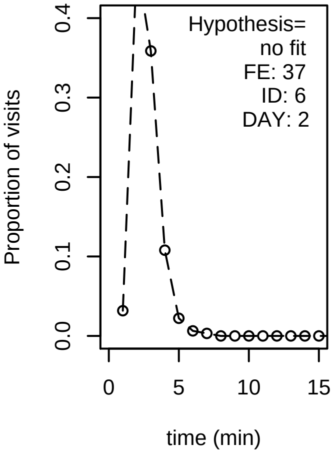
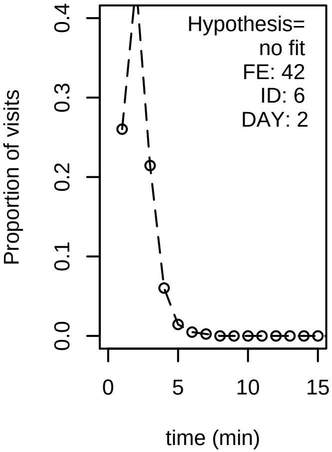
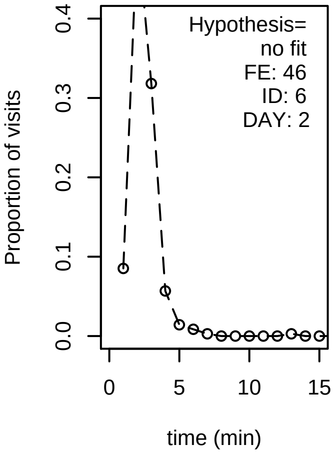
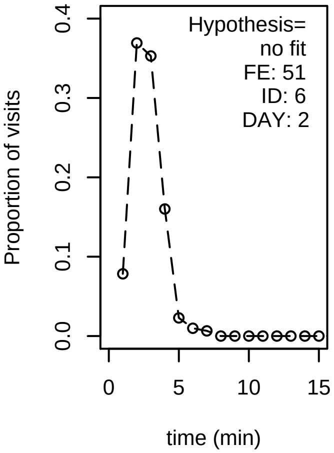
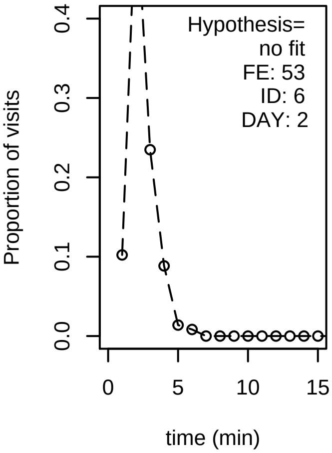
0.1
0.2
0.3
0.4
0
5
10
15
time (min)

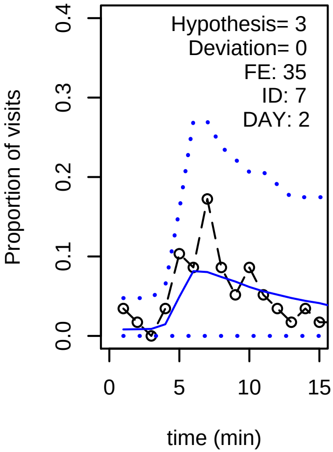

Hypothesis=
no fit
FE: 37
ID: 6
DAY: 2
Proportion of visits
0.0
0.1
0.2
0.3
0.4
0
5
10
15
time (min)


Hypothesis=
no fit
FE: 42
ID: 6
DAY: 2
Proportion of visits
0.0
0.1
0.2
0.3
0.4
0
5
10
15
time (min)


Hypothesis=
no fit
FE: 46
ID: 6
DAY: 2
Proportion of visits
0.0
0.1
0.2
0.3
0.4
0
5
10
15
time (min)


Hypothesis=
no fit
FE: 51
ID: 6
DAY: 2
Proportion of visits
0.0
0.1
0.2
0.3
0.4
0
5
10
15
time (min)


Hypothesis=
no fit
FE: 53
ID: 6
DAY: 2
Proportion of visits
0.0
0.1
0.2
0.3
0.4
0
5
10
15
time (min)


Hypothesis= 3
Deviation= 0
FE: 35
ID: 7
DAY: 2
Proportion of visits
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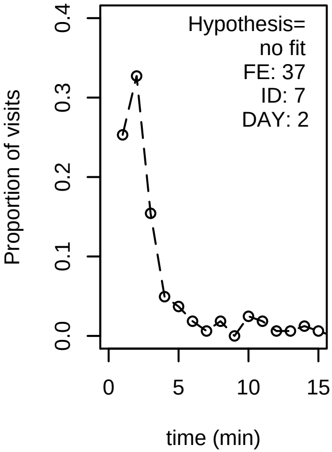
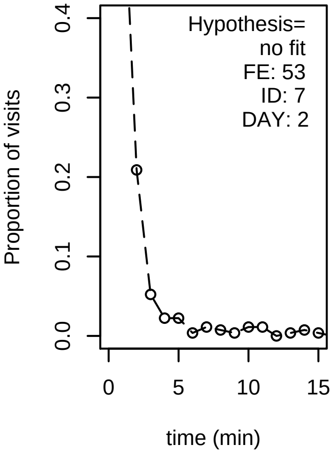
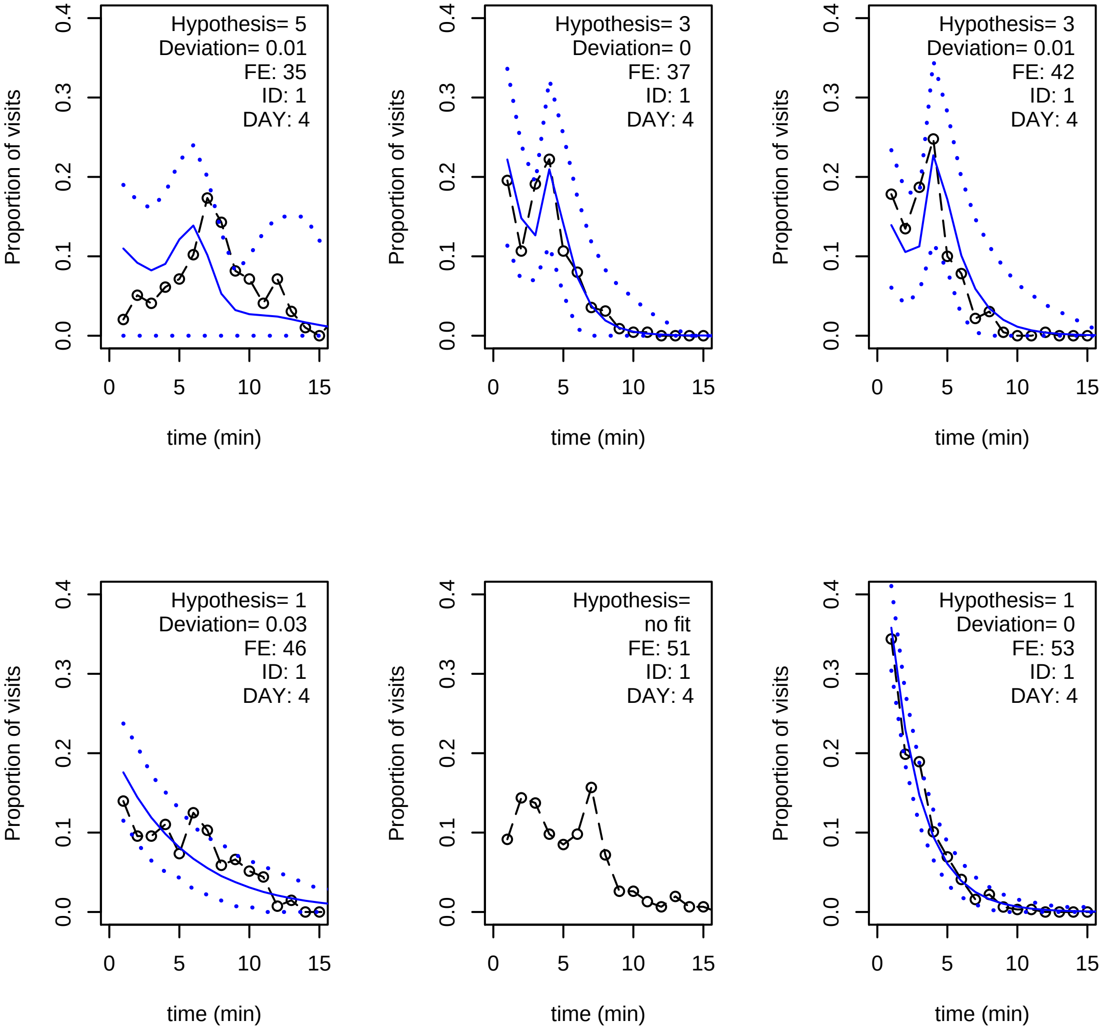
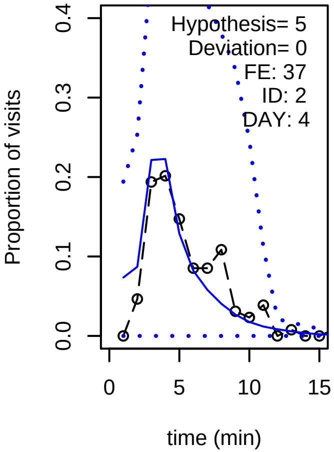
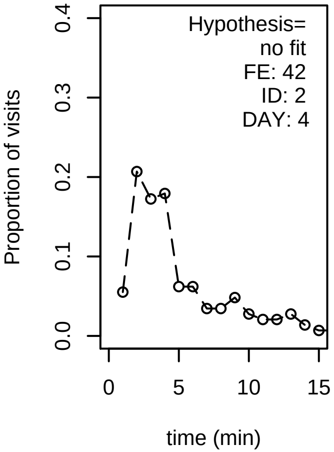
0.2
0.3
0.4
0
5
10
15
time (min)


Hypothesis=
no fit
FE: 37
ID: 7
DAY: 2
Proportion of visits
0.0
0.1
0.2
0.3
0.4
0
5
10
15
time (min)


Hypothesis=
no fit
FE: 53
ID: 7
DAY: 2
Proportion of visits
0.0
0.1
0.2
0.3
0.4
0
5
10
15
time (min)


Hypothesis= 5
Deviation= 0.01
FE: 35
ID: 1
DAY: 4
Hypothesis= 3
Deviation= 0
FE: 37
ID: 1
DAY: 4
Hypothesis= 3
Deviation= 0.01
FE: 42
ID: 1
DAY: 4
Hypothesis= 1
Deviation= 0.03
FE: 46
ID: 1
DAY: 4
Hypothesis=
no fit
FE: 51
ID: 1
DAY: 4
Hypothesis= 1
Deviation= 0
FE: 53
ID: 1
DAY: 4
Proportion of visits
0.0
0.1
0.2
0.3
0.4
time (min)
0
5
10
15


Hypothesis= 5
Deviation= 0
FE: 37
ID: 2
DAY: 4
Proportion of visits
0.0
0.1
0.2
0.3
0.4
0
5
10
15
time (min)


Hypothesis=
no fit
FE: 42
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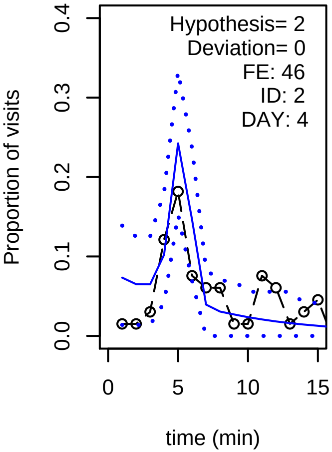
DAY: 4
Proportion of visits
0.0
0.1
0.2
0.3
0.4
0
5
10
15
time (min)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Deviation= 0
FE: 46
ID: 2
DAY: 4
Proportion of visits
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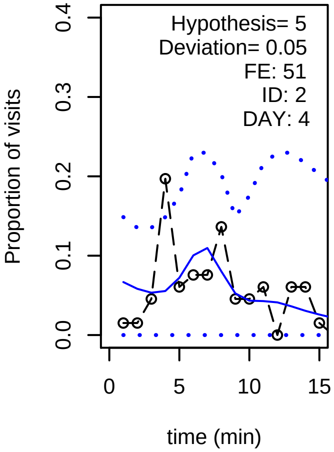
0.2
0.3
0.4
0
5
10
15
time (min)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Deviation= 0.05
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DAY: 4
Proportion of visits
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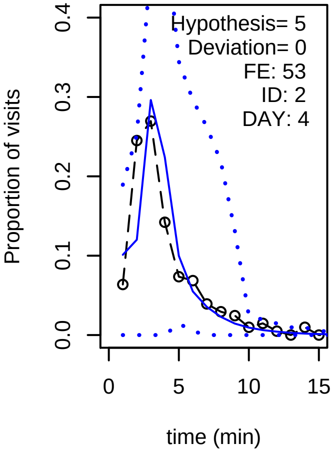
0.2
0.3
0.4
0
5
10
15
time (min)


Hypothesis= 5
Deviation= 0
FE: 53
ID: 2
DAY: 4
Proportion of visits
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0.1
0.2
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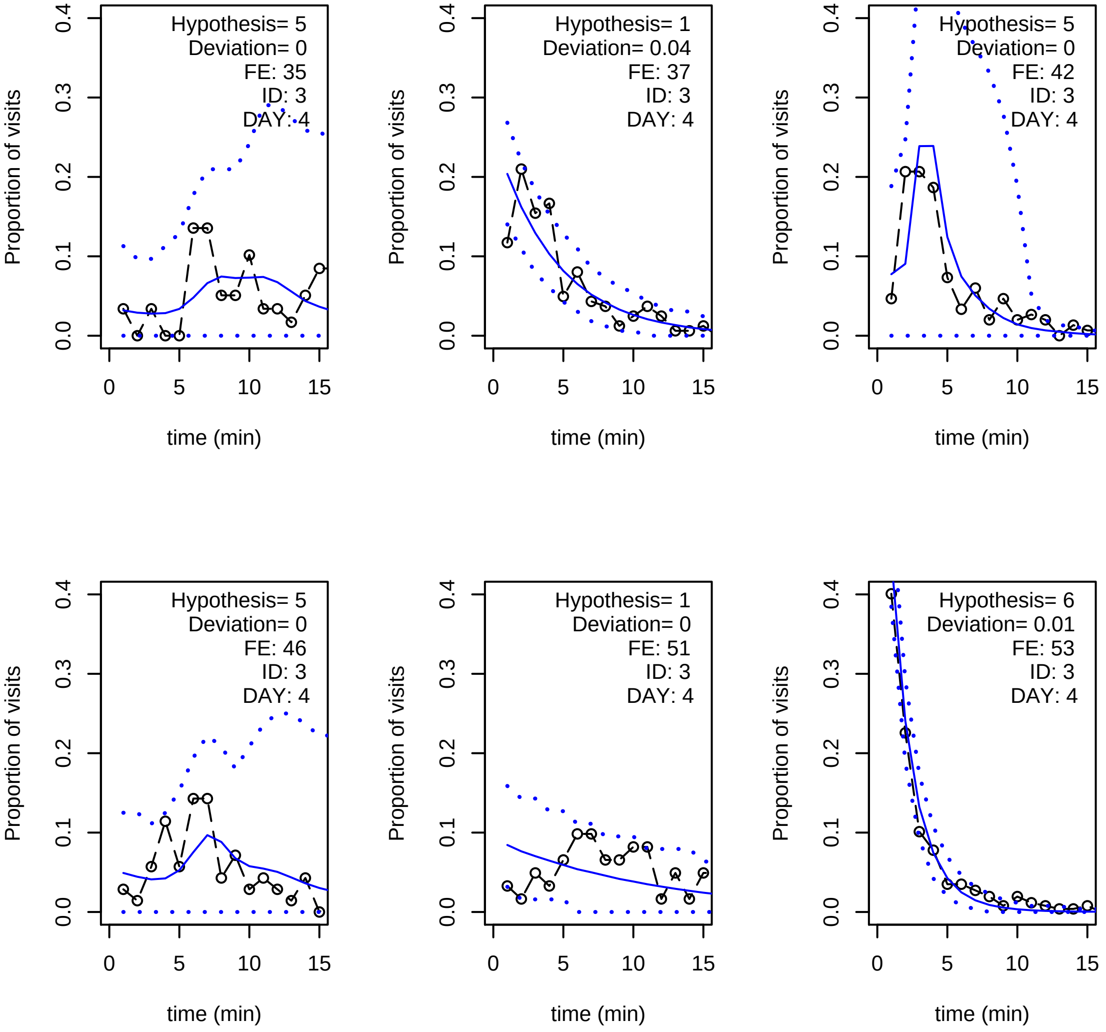
0.4
0
5
10
15
time (min)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DAY: 4
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ID: 3
DAY: 4
Hypothesis= 5
Deviation= 0
FE: 42
ID: 3
DAY: 4
Hypothesis= 5
Deviation= 0
FE: 46
ID: 3
DAY: 4
Hypothesis= 1
Deviation= 0
FE: 51
ID: 3
DAY: 4
Hypothesis= 6
Deviation= 0.01
FE: 53
ID: 3
DAY: 4
Proportion of visits
time (min)
0.0
0.1
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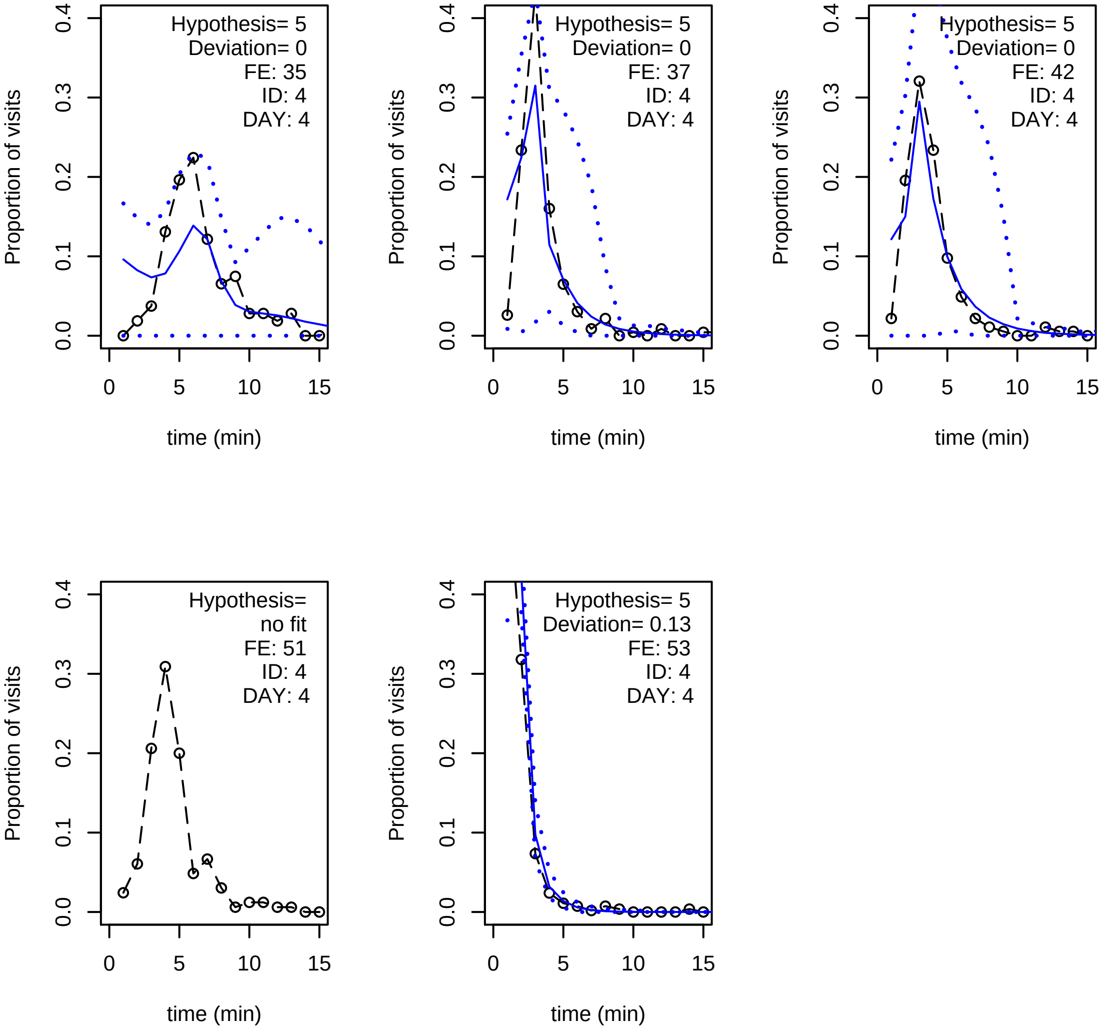
0.3
0.4
0
5
10
15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Deviation= 0
FE: 37
ID: 4
DAY: 4
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Deviation= 0
FE: 42
ID: 4
DAY: 4
Hypothesis=
no fit
FE: 51
ID: 4
DAY: 4
Hypothesis= 5
Deviation= 0.13
FE: 53
ID: 4
DAY: 4
Proportion of visits
time (min)
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0.1
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0.3
0.4
0
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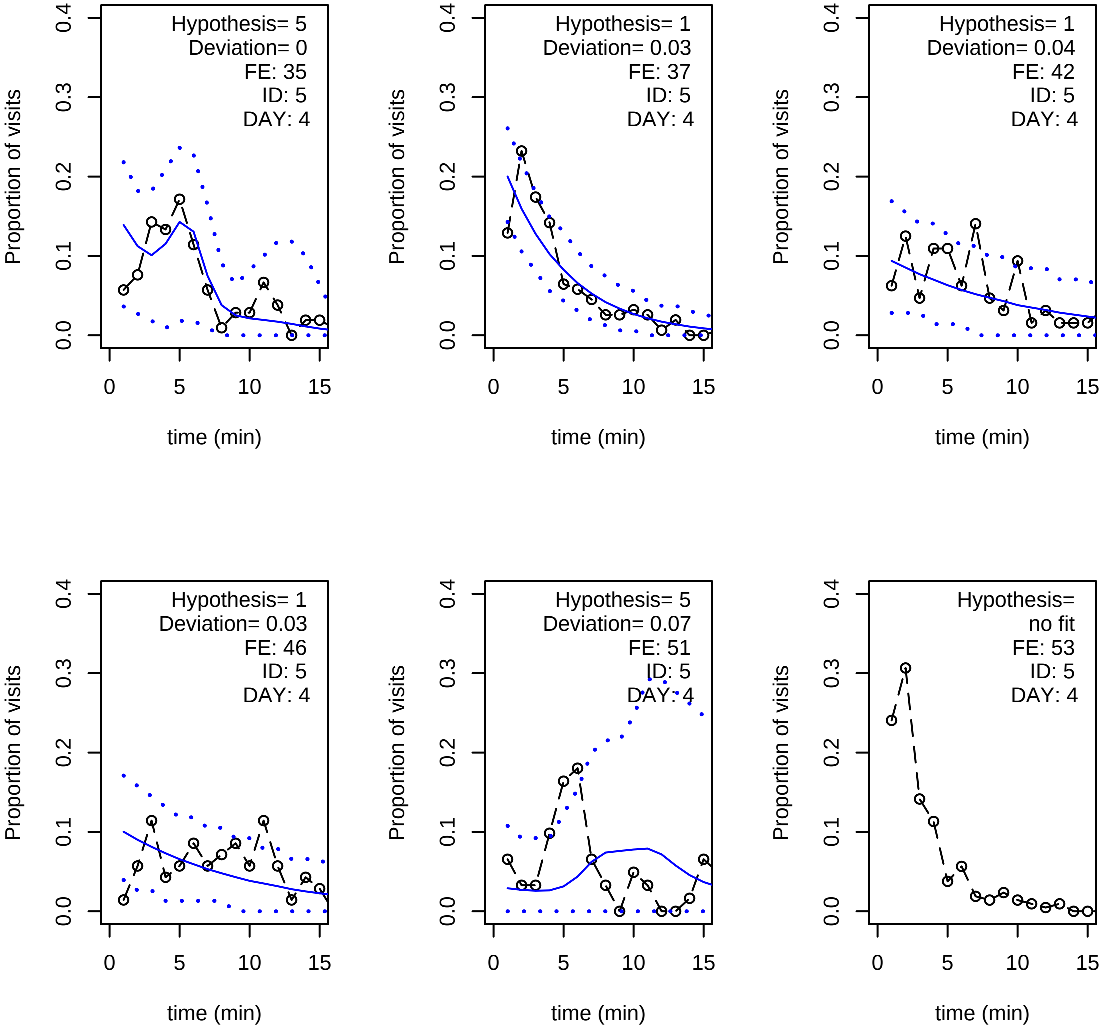
10
15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DAY: 4
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ID: 5
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Hypothesis= 1
Deviation= 0.04
FE: 42
ID: 5
DAY: 4
Hypothesis= 1
Deviation= 0.03
FE: 46
ID: 5
DAY: 4
Hypothesis= 5
Deviation= 0.07
FE: 51
ID: 5
DAY: 4
Hypothesis=
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FE: 53
ID: 5
DAY: 4
Proportion of visits
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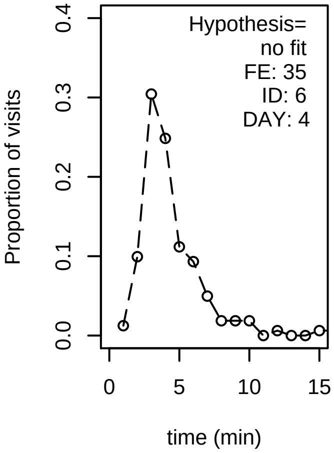
0.2
0.3
0.4
time (min)
0
5
10
15


Hypothesis=
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FE: 35
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DAY: 4
Proportion of visits
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0.1
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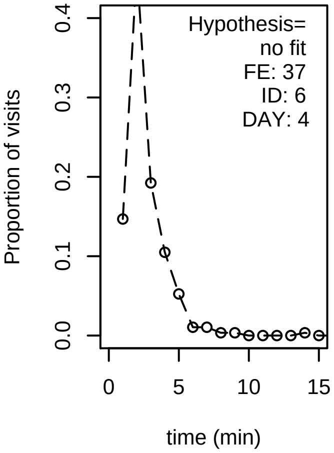
0.4
0
5
10
15
time (min)


Hypothesis=
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FE: 37
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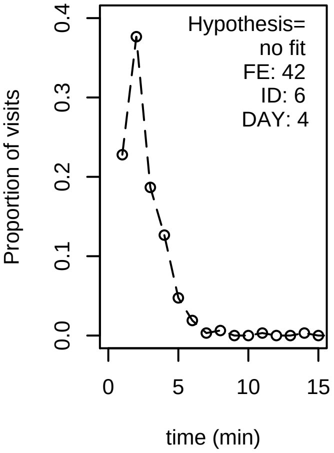
DAY: 4
Proportion of visits
0.0
0.1
0.2
0.3
0.4
0
5
10
15
time (min)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FE: 42
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DAY: 4
Proportion of visits
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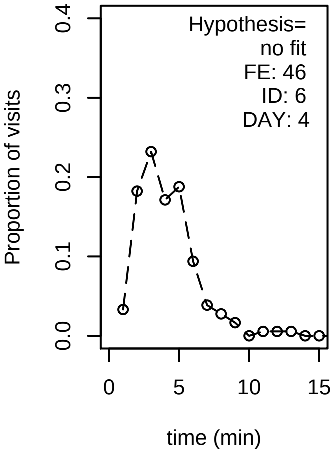
0.3
0.4
0
5
10
15
time (min)


Hypothesis=
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FE: 46
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DAY: 4
Proportion of visits
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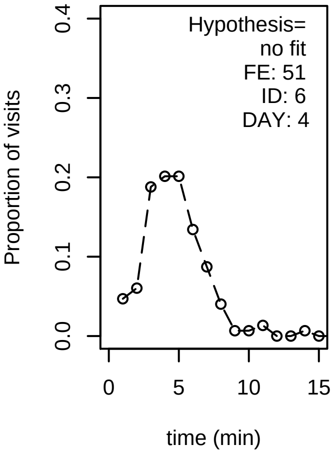
0.4
0
5
10
15
time (min)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Proportion of visits
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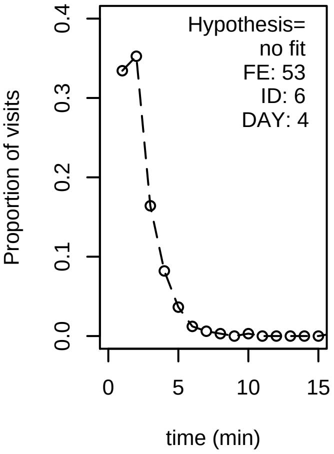
0.4
0
5
10
15
time (min)


Hypothesis=
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FE: 53
ID: 6
DAY: 4
Proportion of visits
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0.1
0.2
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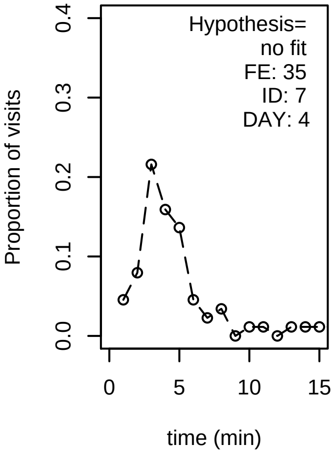
0.4
0
5
10
15
time (min)


Hypothesis=
no fit
FE: 35
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DAY: 4
Proportion of visits
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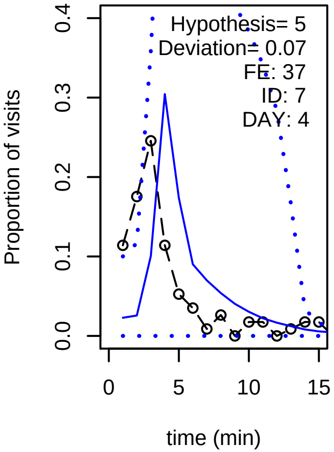
0.2
0.3
0.4
0
5
10
15
time (min)


Hypothesis= 5
Deviation= 0.07
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DAY: 4
Proportion of visits
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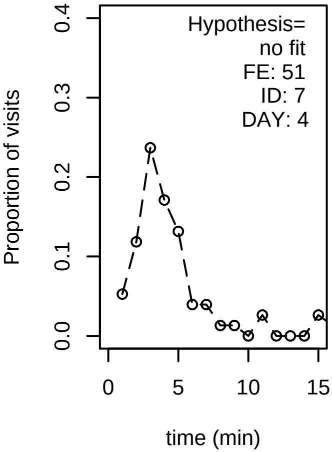
0
5
10
15
time (min)


Hypothesis=
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FE: 51
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DAY: 4
Proportion of visits
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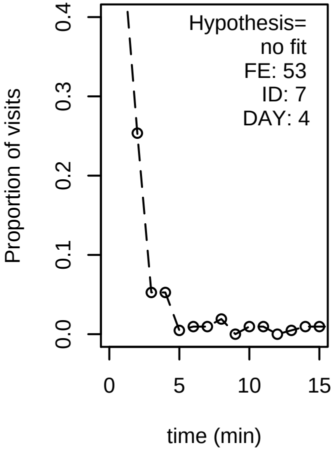
0.4
0
5
10
15
time (min)


Hypothesis=
no fit
FE: 53
ID: 7
DAY: 4
Proportion of visits
0.0
0.1
0.2
0.3
0.4
0
5
10
15
time (min)

Chapter	***Folder***	***File name***	***Content***
1- cue use	LMExperiment	Gesamtvesuchsdesign.xls	Design of Experiement, Position of rewarding feedeers and cue
1- cue use	LMExperiment	MS_Landmark_use_in_a_bat_figures	Summary of figures
1- cue use	LMExperiment\Auswertung	Auswertungsmatrix2.xls	Summary of rawdata in visits of 50
1- cue use	LMExperiment\Auswertung	visits to cued unrewarded feeders	Visits to feeders that had cues but were not rewarded
1- cue use	LMExperiment\Auswertung	R_Ausw_Matrix	R Workspace with summary of the rawdata
1- cue use	LMExperiment\Rohdaten	ZusLMExp2	Summary of rawdata (main summary)
1- cue use	LMExperiment\Rohdaten	A030914.csv	Rawdata ID 1 cues 0, ID 2 cues 0, ID 3 cues 0
1- cue use	LMExperiment\Rohdaten	A030915.csv	Rawdata ID 1 cues 16, ID 2 cues 2, ID 3 cues 4
1- cue use	LMExperiment\Rohdaten	A030916.csv	Rawdata ID 1 cues 2, ID 2 cues 16, ID 3 cues 8
1- cue use	LMExperiment\Rohdaten	A030917.csv	Rawdata ID 1 cues 8, ID 2 cues 4, ID 3 cues 2
1- cue use	LMExperiment\Rohdaten	A030918.csv	Rawdata ID 2 cues 8, ID 3 cues 16
1- cue use	LMExperiment\Rohdaten	A030920.csv	Rawdata ID 2 cues 0, ID 3 cues 0
1- cue use	LMExperiment\Rohdaten	A030927.csv	Rawdata ID 4 cues 0, ID 5 cues 0
1- cue use	LMExperiment\Rohdaten	A030928.csv	Rawdata ID 4 cues 16, ID 5 cues 2
1- cue use	LMExperiment\Rohdaten	A030929.csv	Rawdata ID 4 cues 2, ID 5 cues 16
1- cue use	LMExperiment\Rohdaten	A030930.csv	Rawdata ID 4 cues 8, ID 5 cues 4
1- cue use	LMExperiment\Rohdaten	A031001.csv	Rawdata ID 4 cues 4, ID 5 cues 8
1- cue use	LMExperiment\Rohdaten	A031002.csv	Rawdata ID 4 cues 0, ID 5 cues 0
1- cue use	LMExperiment\Rohdaten	A031016.csv	Rawdata ID 6 cues 0
1- cue use	LMExperiment\Rohdaten	A031017.csv	Rawdata ID 6 cues 16
1- cue use	LMExperiment\Rohdaten	A031019.csv	Rawdata ID 6 cues 2
1- cue use	LMExperiment\Rohdaten	A031020.csv	Rawdata ID 6 cues 8
1- cue use	LMExperiment\Rohdaten	A031021.csv	Rawdata ID 6 cues 4
1- cue use	LMExperiment\Rohdaten	A031024.csv	Rawdata ID 6 cues 0

Appendix C

Chapter	***Folder***	***File name***	***Content***
1- cue use	LMExperiment\Rohdaten	A031025.csv	Rawdata ID 7 cues 0
1- cue use	LMExperiment\Rohdaten	A031026.csv	Rawdata ID 7 cues 16
1- cue use	LMExperiment\Rohdaten	A031027.csv	Rawdata ID 7 cues 2
1- cue use	LMExperiment\Rohdaten	A031028.csv	Rawdata ID 7 cues 8
1- cue use	LMExperiment\Rohdaten	A031029.csv	Rawdata ID 7 cues 4
1- cue use	LMExperiment\Rohdaten	A031031.csv	Rawdata ID 7 cues 0
2- amount	MengenExperiment	psychometric function	R Code for Psychometric function
2- amount	MengenExperiment	MS_Discrimination between figures	Summary figures
2- amount	MengenExperiment\Auswertung	Auswertung letze 6 Tiere	Summary of rawdata of 7! Animals
2- amount	MengenExperiment\Auswertung	amount_R	R data file for psychometric function
2- amount	MengenExperiment\Rohdaten	A041023.csv	Raw data ID 1-4
2- amount	MengenExperiment\Rohdaten	A041215.csv	Raw data ID 5,6
2- amount	MengenExperiment\Rohdaten	A041217.csv	Raw data ID 7
3 - peak	PeakExperiment\Rohdaten11s	4Tiere_10Tage	Summary 11s Peak schedule ID 1-4
3 - peak	PeakExperiment\Rohdaten11s	A5	Summary ID 5 11 s Peak schedule
3 - peak	PeakExperiment\Rohdaten11s	A6	Summary ID 6 11 s Peak schedule
3 - peak	PeakExperiment	MS_Peak_figures	Summary figures
3 - peak	PeakExperiment\Rohdaten5s	all_ids_ulf	Summary ID 1-6 5 s Peak schedule
3 - peak	PeakExperiment\Rohdaten5s	S050407.csv-S050415.csv	Raw data 5 s Peak schedule ID 1
3 - peak	PeakExperiment\Rohdaten5s	S050420.csv-S050427.csv	Raw data 5 s Peak schedule ID 2
3 - peak	PeakExperiment\Rohdaten5s	S050423.csv-S050504.csv	Raw data 5 s Peak schedule ID 3
3 - peak	PeakExperiment\Rohdaten5s	S050513.csv-S050519.csv	Raw data 5 s Peak schedule ID 4
3 - peak	PeakExperiment\Rohdaten5s	S050707.csv-S050714.csv	Raw data 5 s Peak schedule ID 5,6

Chapter	***Folder***	***File name***	***Content***
3 - peak	PeakExperiment\Rohdaten11s	S041222.csv-S041230.csv	Raw data 11 s Peak schedule ID 1-4
3 - peak	PeakExperiment\Rohdaten11s	S050122.csv-S050202.csv	Raw data 11 s Peak schedule ID 5,6
3 - peak	PeakExperiment\Auswertung	5_11_20_Peak_base2	R Data File with only empty trials
4- Secretion	Sekretionsexperiment	MS_Secretion_figures	Summary figures
4- Secretion	Sekretionsexperiment\Auswertung	AppendixA	Appendix A of Thesis Summary of behaviour at different feeders
4- Secretion	Sekretionsexperiment\Auswertung	Appendix B1	Appendix B of Thesis Part I empirical and theoretical distributions of revisit time
4- Secretion	Sekretionsexperiment\Auswertung	Appendix B2	Appendix B of Thesis Part II empirical and theoretical distributions of revisit time
4- Secretion	Sekretionsexperiment\Auswertung	A_Sekretion_A1234567	Summary of revisit intervals of single animals and single feeders and phases (Single workbook tables represent the animal ids)
4- Secretion	Sekretionsexperiment\Model	summary_hyp	Summary of the simulation of hypotheses
4- Secretion	Sekretionsexperiment\R	Modellierung_sec_with_decay_process9	R Data file with simulation and empirical data and code for figures
4- Secretion	Sekretionsexperiment\R	time_analysis_cox_reg	Cox Regression for revisit time analysis
4- Secretion	Sekretionsexperiment\R	base_count_net_gain	R file for comparison of different phases
4- Secretion	Sekretionsexperiment\Rohdaten	Summary_A1234567TRUE2.1	Summary file for the raw data of the seven animals
4- Secretion	Sekretionsexperiment\Rohdaten	S050411-S050414	Secretion ID 1
4- Secretion	Sekretionsexperiment\Rohdaten	S050504-S050507	Secretion ID 2
4- Secretion	Sekretionsexperiment\Rohdaten	S050511-S050514	Secretion ID 3
4- Secretion	Sekretionsexperiment\Rohdaten	S050603-S050514	Secretion ID 4
4- Secretion	Sekretionsexperiment\Rohdaten	S050611-S050513 S050623	Secretion ID 5
4- Secretion	Sekretionsexperiment\Rohdaten	S050707-S050710	Secretion ID 6
4- Secretion	Sekretionsexperiment\Rohdaten	S050707-S050724	Secretion ID 7

Chapter	***Folder***	***File name***	***Content***
4- Secretion	Sekretionsexperiment\MCPoisson		this folder contains the commented delphi code for the simulation
5- variance	CRExperiment	EichkurveVentilblüte	Calibration of open field feeders
5- variance	CRExperiment\Auswertung	Result_Matrix	Summary visits to variable and constant feeders for each animal
5- variance	CRExperiment\Auswertung	Matrix_SAS_Schwirrflug	Hover time durations
5- variance	CRExperiment\Daten	U040204	Raw data all Ids
5- variance	CRExperiment\Daten	U040205	Raw data all Ids

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82319 Starnberg
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Marital Status: married, 1 child (1 year)

Education

2002 -	Ph.D. student at the Ludwig Maximilans University Munich in cooperation with the Max-Planck Institute for Ornithology Title of Ph.D. thesis: “Bat time stories: Decision-making in spatio-temporally predictable environments ”
2005	Participated in RISE exchange program of the DAAD and supervised an American student for three months
2004	5 week research visit to La Selva Biological Station, Costa Rica
2003	DZG – Workshop Population Ecology: Modelling of Population Dynamics
2003	Workshop “Cognition and the Evolution of Learning”, Fribourg CH
2002	Diploma in Biology (Grade: “sehr gut”) at the University of Kiel
1996-2002	Studying Biology at the University of Kiel
1995	Abitur at the Dahlmannschule Bad Segeberg (Grade: 2.0)

Work History

2002-	Research associate in the ecological neurobiology research group at the Ludwig Maximilians University in Munich
2002	Graduate assistant at the department of ecology at the University of Kiel (assistant in graduate course population ecology)
1997-2001	Graduate assistant at the department of phytopathology at the University of Kiel (field technician, plant monitoring)
2000/2001	Planning and production of several short educational films for the Institute of educational sciences at the University of Kiel
1995-1996	Military service

Extracurricular Activities

Acting in and directing several theatre plays (15 up to date). The latest project involved directing and staging Falk Richter’s “Electronic City” in November 2004 at the Institute for theatre sciences at the Ludwig Maximilians University in Munich.
Other hobbies include: Filming, skiing and mountain hiking

General Skills

Languages:	German (native speaker), excellent written and spoken skills in English, Basic Skills in French and Norwegian
Programming Languages:	advanced skills in Delphi, Visual Basics; basic skills in C/C++
Computer programs:	excellent skills in MS-Office, advanced skills in SAS, SPSS, Matlab, R
Statistics:	advanced to excellent skills in multivariate and regression statistics, repeated measures designs
Modelling:	basic to advanced skills in stochastic dynamic programming and genetic algorithms

International conferences

XXII International Congress of Entomology, Brisbane, AUS, 2004. Invited oral presentation : *Hoffmeister, T.S., Thiel, A., Tölch, U., Kersch, M.F., Piening, J.J.* How parasitoids read the news: information use in a patchy world;
13th International Entomophagous Workshop, Tucson, AZ, USA 2003. Oral presentation: *Hoffmeister, Thiel, Kolß, Tölch, Kersch* How parasitoids can estimate habitat quality and respond to information cues within and between patches;

National Conferences

Arbeitsgruppentreffen der deutschen Fledermausforscher , Blaubeuren, 2005. Oral presentation: *Tölch, U., Winter, Y.,* Foraging in complex environments: The adaptive value of seemingly suboptimal decisions;

Jahresversammlung der DZG, Berlin, 2003. Oral presentation: *Hoffmeister,T.S., Kolß, M., Frank-Kersch, M., Tölch, U.,* Is it good to respond to bad experience? – Insights from parasitoid wasps;