Serial reversal learning in nectar-feeding bats

Shambhavi Chidambaram1,2, Sabine Wintergerst3, Alex Kacelnik4, Vladislav Nachev1, York Winter1,2\*

1 Institute of Biology, Humboldt University, Berlin, Germany

2 Berlin School of Mind and Brain, Humboldt University, Berlin, Germany

3 Fairchild Tropical Botanic Garden, Miami, USA

4 Department of Zoology, University of Oxford

**\*For correspondence:** [york.winter@hu-berlin.de](mailto:york.winter@hu-berlin.de)

**Present Address:** Institute of Biology, Humboldt University, Philippstr. 13, 10115 Berlin, Germany

# Abstract

Animals that show flexibility in their behavioural responses to environmental change have a strong advantage in foraging for food. We aimed to explore this ability in Commissaris’s long-tongued bat through a spatial serial reversal learning task. Wild bats were trained to obtain rewards from two artificial flowers. At any given time only one of the flowers provided rewards. After the bats had experienced the rewarding properties of the flowers for some time, a reversal happened: the rewarding flower became non-rewarding and *vice versa*. These reversals of rewarding properties occurred repeatedly.

We found that the bats detected and responded to the reversals of reward properties: when a food location suddenly dried up the bats abandoned visiting it and switched to the alternative, showing a near-exclusive preference for the rewarding option. The bats switched to the rewarding flower more swiftly with each successive experience of a reversal, reaching a plateau in their performance by the fifth reversal they experienced. The proportion of visits to the rewarding flower increased overall, driven by the increase in the proportion of rewarded visits immediately after each reversal. Our results are consistent with a high capacity for behavioural flexibility in nectar-feeding bats.

# Introduction

Many animals live in environments where food availability changes frequently and often unpredictably. Nectar-feeding animals mainly forage on flowering plants and the food resource they provide: nectar and pollen. Though flowers are stationary, they bloom seasonally and single flowers on plants themselves wither and die every day or every few days, altering their efficacy with time as food resources. Thus, nectar-feeding animals face the challenge of exploiting resources that continually change with time but are relatively predictable in space. These animals need to detect the changing reward contingencies in their environment and adjust their behaviour accordingly.

Behavioural flexibility is an ability to cope with such changes. The word ‘flexibility’ has been used to mean many different things in the animal behaviour literature (often inconsistently – Audet and Lefebvre 2017), and one interpretation of the word is similar to the concept of elasticity: behavioural patterns that can be repeatedly and readily reversed (Bond, Kamil, and Balda 2007). An experimental protocol that has been widely used to test for and demonstrate this sort of flexibility is reversal learning (Izquierdo et al. 2017).

In a reversal learning task an animal must first learn about multiple stimulus-response associations, such as two spatial locations that can be approached to obtain a potential reward. The animal must then discriminate between these associations in its behaviour, according to the strength of that association. This is first-order learning (Balsters and Ramnani 2011). When only one of the two options is rewarding, this is the only one a reward-maximizing animal should respond to. When reinforcement at this location stops, the animal should abolish its current behaviour. It is this ability to abruptly terminate a repeated behaviour and switch to another behaviour that the animal needs to have for efficient exploitation of the available resources. The information contained in the absence of an expected reward becomes a stimulus in itself. A successful animal associates this non-reward stimulus with the appropriate response, which is the inhibition of its previous behaviour and reorientation to an available alternative. In a serial reversal learning procedure the reward contingencies of two options reverse repeatedly: one option is rewarding and the other is not; then the rewarding option stops yielding reward and the previously non-rewarding option becomes rewarding. The question then is: can an animal detect the rule of the environment that dictates change in reward contingencies, learn which cue indicates that change, and respond to this “cue of change?” In a serial reversal paradigm a theoretical animal which collects the maximum possible reward makes exactly one error per reversal.

We carried out a serial reversal learning task with Commissaris’s long-tongued bat, (*Glossophaga commissarisi*), which, seasonally, primarily feeds on flower nectar (Tschapka 2004). Flower visitors like these bats may often experience reversal situations in their natural environment. A flower full of nectar may remain rewarding for multiple visits before it is empty. The flower visitor should then seek another flower. However, at a later time-point, when ongoing secretion has replenished nectar, a previously visited flower is rewarding again. In our experiment the bats were offered two potentially rewarding options. The options were separated in space and their spatial location was the cue to indicate their reward properties at any moment. Glossophaginebats areknown to have excellent spatial memory (Stich 2004a, 2004b; Thiele and Winter 2005) so no other cue was necessary. At the start of the night, only one of the options was rewarding (the ‘S+’ option), and the other was not rewarding (the ‘S-’ option). After a certain number of visits had been made by the bats, the reward contingencies reversed without any signal or cue to the bats: the previously rewarding option was now unrewarding and the previously unrewarding option was rewarding. This reversal happened five times in a night.

It is well known that bats alter their preference between reward sources according to their transient rewarding properties and thus show first-order learning for spatial locations (Stich 2004a, 2004b; Winter, von Merten, and Kleindienst 2005; Tölch and Winter 2007; Nachev and Winter 2012; Nachev et al. 2017). Thus, the aim of our present experiment was to test if bats could learn to respond to stimuli that indicate that their environment has changed by then changing their own behaviour. Faced with the occurrence of successive reversals, would the bats change their behavioural allocation between the two potentially rewarding options with increasing speed? Further, we were interested to see if the abruptness of switching from one option to another would decrease to the theoretical optimum, i.e., occurring after just one unrewarded visit per reversal.

We report results from a series of five reversals, in an effort to find out whether bats switched to the newly rewarding option after each reversal with increasing efficiency.

# Methods

## Study site and subjects

The experiment took place at La Selva Biological Field Station, Province Heredia, Costa Rica in June-July 2017. Bats of the species *Glossophaga commissarisi* were captured from the wild and retained in a flight cage through the experiment. The bats were attracted to a particular location in the forest using chicken-feeders filled with sugar-water (see **Reward**) as bait. The feeders had cotton swabs soaked in dimethyl disulphide on them, a chemical attractant produced by many bat-pollinated flowers (von Helversen, Winkler, and Bestmann 2000) and then caught in mist-nets. The bats were sexed on capture and housed in two outdoor, meshed flight-cages (4 x 6 m) under ambient light conditions. All individuals were weighed and marked with radio frequency identification (RFID) tags placed as collars around their necks.

A total of 16 bats participated in the main experiment and the first stage of the experiment began on the same night the bats entered the cages. A group of four experimental bats of the same sex were placed in a flight cage together. Two such groups were run in parallel, one in each flight-cage so the data were collected simultaneously. At the end of the experiment, the RFID collars were removed and the bats were released back into the wild. All the data collection was completely automatized. Two of the bats did not drink a sufficient amount of sugar-water to meet minimum energy requirements. These two bats were released before the end of the experiment and not replaced, and the data from these two individuals were not analyzed. Thus, 14 bats (7 males and 7 females) completed the experiment. Permission for this research was granted by Sistema Nacional de Areas de Conservación (SINAC) at the Ministerio de Ambiente y Energía (MINAE), Costa Rica.

## Experimental Setup

### Reward

The reward received by the bats during the experiment was also their main source of food. The reward was a 17% w/w sugar solution, hereafter referred to as ‘nectar.’ The sugar consisted of a 2:1 mass-mixture of fructose and glucose, an approximation of the floral nectar-composition of chiropterophilous plants (Baker, Baker, and Hodges 1998). Every night, the four bats of a flight cage were also given *ad-libitum* access to supplemental food: 0.25 mL of honey and 0.3 g of milk powder (Nido 1+, Nestle, Switzerland) per bat dissolved in 1 mL of water per bat. The bats in each cage were also given a small bowl of locally sourced bee pollen.

### Flower and feeder setup

Each flight cage had a square frame in the center (2 × 2 m), fixed 1.5 m above the ground. Eight reward-dispensing devices - hereafter referred to as ‘flowers’ - were fixed two on each side of the square (Figure 1) with a distance of 40 cm between adjacent flowers. At this distance, bats can easily discriminate neighbouring flowers (Thiele and Winter 2005). Each flower had the following parts: a circular RFID antenna mounted at the end of a plastic cylinder that constituted the artificial flower; an infra-red photo gate; and an electronic pinch valve through which a silicon tube was placed and fixed to the base of the flower.

A stepper-motor syringe pump was placed in the center of the square in each cage with a 25 mL Hamilton glass syringe (Sigma Aldrich, Germany). The step volume of the two pumps differed slightly: the pump in Cage 1 delivered 2.11 L per step of the stepper-motor, and the pump in Cage 2, 3.33 L per step. The glass syringe was connected to the tubing system of the flowers through five pinch valves (Nachev, Stich, and Winter 2012). The pinch valves controlled the flow of liquid from the pump to the flower system and from a reservoir of liquid to the pump. The reservoir (500 mL bottle, Roth, Germany) was filled with fresh nectar every day and was connected to the syringe through the valves.

Every day at around 1000 h by an automated routine, the system was emptied from the old nectar, it was rinsed and filled with plain water until 1500 h, when it was filled again with fresh nectar. Twice a week, the system was filled with 70% ethanol for an hour to prevent microbial growth, then repeatedly rinsed with water.

When a tagged bat approached a flower, its individual number was read. If the bat then poked its nose into the flower and interrupted the light beam, this could trigger the release of a reward. The flowers were programmed such that each bat could trigger rewards at only two unique flowers out of the array of eight. The pinch valve opened, and the pump moved the correct number of pre-programmed steps to dispense nectar to the base of the flower. The bat could easily hover in front of the flower and lick up the nectar. A reward was given only when both events occurred, i.e., the RFID reader identified a selected bat and the photo gate was triggered. The flowers and the pump were connected to a Windows PC, which ran the experimental programs and the program used to automatically flush, clean and fill the pump and tubing system (PhenoSoft Control, PhenoSys, Germany).

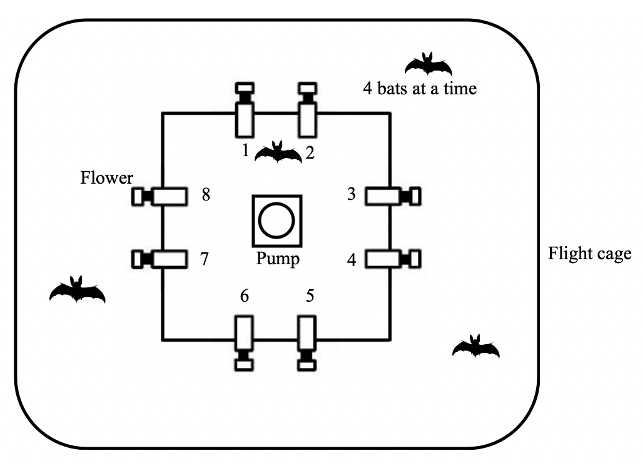


Figure 1: Schematic of the cage and flower set-up (not drawn to scale)

## Experimental procedure

Out of the array of eight flowers, each bat was uniquely assigned two adjacent flowers on the same side of the square frame which were programmed to reward only one of the four bats in the cage. After the system was filled with fresh nectar at 15:00 h, the program was launched at approximately 17:00 h and left running for data-collection till the next morning. Thus, the bats could begin visiting the flowers to collect a reward whenever they chose, which was at nightfall at approximately 18:00 h every night. During the main experiment, each bat could make a maximum of 300 rewarded visits a night.

During the course of the night, when the syringe of the pump had been emptied, the pump re-filled automatically. This event happened only once every night and it took 4.5 minutes (SD = ±0.18) for the cage 1 pump, and 2.4 minutes (SD = ±0.04) for the cage 2 pump.

About 1 % (SD = ±0.74) of all visits made by the bats were wrongly unrewarded: a bat did not receive a reward even when the visit was made to a flower assigned to it that was supposed to be rewarding at the time. This happened either during the pump refill times or when the pump was moving to reward a visit made by another bat that happened almost at the same time. Such events did not count towards the total of 300.

## Experimental design

The experiment proceeded through the following stages.

### Training

On the night the naïve bats were captured and placed into the flight cages, they could receive a reward from any of the flowers whenever they visited them throughout the night. To enable the bats to find the flowers, a small cotton pad soaked in dimethyl disulphide was placed on each flower to encourage the bats to explore the flower heads for nectar food, interrupt the photo gate, and trigger a nectar reward. By the end of the night, all the bats had found the flowers and learned to trigger rewards.

The next stage of training involved assigning the bats uniquely to two out of the eight flowers in the array. For an individual animal, only the two flowers assigned to it would elicit rewards from this stage of training until the end of the experiment. This stage was similar to the previous one, except the bats could only trigger a reward at their two assigned flowers. The chemical attractant was not used.

To ensure that the bats were familiar with both flowers assigned to them, the bats went through one final stage of training: forced alternation. The bats received a reward at one of the two flowers for one trial, and then could only receive reward at the other flower for the next trial. In this way the bats had to alternate between the two flowers every single trial. There was no learning criterion to be met at this stage.

### Serial Reversal Learning Task

In the serial reversal learning task, the bats had continuous access to two flowers: one that gave a 40 L nectar reward, and one that remained empty. The location of the rewarding flower was not cued; however, after completing the alternation training phase, each bat knew the locations of both flowers that were potentially rewarding to it. After a bat had made 50 visits in total to the two flowers, a reversal occurred: the previously rewarding flower became the non-rewarding flower and *vice versa*. Importantly, only visits to the two flowers assigned to a bat counted towards the visit tally, but the distribution of visits between these two flowers did not have any effect. Each set of 50 visits to the assigned two flowers, either at the start of each night or between reversals, was termed a ‘block.’ There were six blocks and five reversals per night unless the bat ceased visiting earlier. This was repeated for three consecutive nights. The same flower started the sequence every night. Consequently, the last flower to be rewarding one night was non-rewarding at the start of the next. This paper focuses on the first night, when the bats first experienced the reversal protocol. Data from the second and third nights are shown in the supplementary material.

## Data analysis

The raw data collected during this study were the computer-logged events of the visits made by the bats to the flowers. Each event included the time stamp, animal ID, photo gate interruption duration and the volume of nectar dispensed. The bats made some visits and approaches to the flowers that were not assigned to them; however, these were in the minority, and were not considered for the analysis (see Supplementary Material for details). An experimental night had five reversals, one at the end of each of the first five blocks; the end of the last block was the end of data-collection for the night. Each block was further divided into five bins of ten visits, in order to examine the bats’ behaviour within each block. R (version 3.6.3, R Development Core Team 2020) was used for all statistical analyses and creation of plots.

All the statistical models were fitted in a Bayesian framework using Hamiltonian Monte Carlo in the R package brms (Bürkner 2017) which is a front-end for rstan (Carpenter et al. 2017). Generalized linear mixed models (GLMMs) were used for the analyses (see Supplementary Materialfor the technical details of the model fitting). We report here the mean as a measure of central tendency and the 89% quantile-based credible intervals for the intercept and slope coefficients (89% boundaries are the default for reporting credible intervals – McElreath 2020). To aid in the interpretation of the model parameters we also present plots of the conditional effects of some of the predictor variables.

We focused our analysis on the sequence of five reversals of the first experimental night because behaviour reached a stable asymptote within this period (Supplementary Material).

Our aim was to quantify how swiftly the bats switched from the previously-rewarding option to the newly-rewarding one after a reversal. The first block of the night was not included in the analysis, as no reversal had been experienced at the start of this block. The data were grouped into bins of 10 visits each and we fit a generalized linear mixed-model (GLMM) to the data to investigate the effects of number of reversal, bin, and their interaction, on the proportion of visits to the rewarding flower. The proportion of visits to the rewarding flower was calculated as the number of visits to the S+ divided by total number of visits to both the S+ and S-, and we denoted this as the Proprew.

For some results we report 95% confidence intervals, as opposed to credible intervals, and these are noted specifically. The confidence intervals were calculated by non-parametric bootstrapping without assuming a normal distribution of the data, using the Hmisc package (Harrell, 2021).

## Data availability

All data and analysis code are available online at …

# Results

## Bats made a consistently high proportion visits to the rewarding option

The bats made a very high number of visits to the rewarding option: 83.3% [95% CI 82.6, 84.1] overall. When a reversal occurred the bats abandoned the option that had been rewarding until then and switched to making most of their visits to the newly-rewarding option (Figure 2a). A consistent pattern emerged over all the blocks: a sharp decrease in the proportion of visits to the previously-rewarding option immediately following a reversal, then a rapid increase in visits to the newly-rewarding option.

At the start of the experiment, in the first bin of ten visits when the bats had not experienced the reward contingencies of the flowers on that night, the Proprew (the proportion of visits to the rewarding option) averaged across individuals was at chance level: 54.5% [95% CI 46.8, 62.3], about 5 out of the 10 visits. Within the next ten visits however, Proprew increased to 92.1% [95% CI 87.1, 96.4] and by the last bin of this first block was 99.3% [95% CI 97.9, 100]. Immediately after the first experience of a reversal, the Proprew dropped down to 13.6% [95% CI 8.4, 18.8] in the first ten visits, but came back *Chart, line chart

Description automatically generated*up to 96.4% [95% CI 92.9, 99.3] by the last bin of this block of fifty visits (Figure 2b).

*Figure 2: Visits to the rewarding one of two options. Shading shows 95% confidence intervals, and numbers indicate the total number of bats that participated in a block. Data are average proportions for bins of ten visits averaged over all the individuals that made visits in each bin. Vertical dashed lines show reversals a) Data indicated by white circles in the first block were before the bats had experienced any reversals; black circles after the experience of a reversal b) Data indicated by triangles are proportions of rewarded visits in the first bin of 10 visits in a block; by squares, in the last bin of 10 visits in a block*

## Bats switched to the rewarding option faster as they experience more reversals

Perseverative visits are visits to the previously-rewarding option after a reversal has occurred. If the animals switched to the rewarding option faster after a reversal, we expected to see a decrease in the number of perseverative visits as the bats experienced more reversals. This means that the number of rewarded visits immediately after a reversal should increase. The proportion of visits to the rewarded flower in the first bin of 10 visits after a reversal increased as the bats experienced more reversals, more so than in any other bin. This conclusion was visually evident in the raw data (Figure 2b), and held up by the statistical analysis (Figure 3).

The Proprew in the first bin of 10 visits after a reversal increased significantly as the bats experienced more reversals (Figure 3a and 3b). This effect was present in the second bin of 10 visits (visits 11 - 20 of the same block) as well, but by the third bin there was no further change (Figure 4b). This result indicated that the bats switched to the rewarding flower with increasingly fewer number of visits, as they experienced successive reversals.

The effect of number of reversals on the Proprew persisted even when the data from the first reversal were removed from the analysis (see Supplementary Material, figure S3). That is, the effect of the number of reversals was *not* driven mainly by the first block after the reversal, where the effect was largest (Figure 4b), but instead by each successive experience of a reversal.

At the end of each block, i.e., just before the next reversal, the bats visited the rewarding flower almost exclusively. If the bats had learnt the constant number of 50 trials in a block, they could have developed anticipatory behaviour, expressed as starting to switch to the non-rewarding feeder towards the end of each block before the reversal. This would have shown up in the data as a decrease in the number of rewarded visits during the last bin of a block, developing over the course of the experiment. There was no evidence of such anticipatory visits.

Chart, line chart

Description automatically generatedChart, table

Description automatically generated with medium confidence

**a)**

**b)**

Figure 3: a) Forest plot of the regression coefficients from the model of the effect of reversal and 10-visit bin on the visits to the rewarding flower. Data are means and their 50% and 89% credible intervals of the posterior distributions of the slope coefficients, with their values given on the right b) Conditional effects plot from the model of the effect of reversal and 10-visit bin on the visits to the rewarding flower showing the effect of reversal and bin, sampling from the posterior distribution.

At the end of the first night the bats’ choice behaviour just after a reversal did not change any further as an effect of repeated reversal experience (see Supplementary Material, figure S4). Instead, from this point on the bats switched rapidly and consistently to the rewarding flower after a reversal, and made more than 50% of their visits to the rewarding option by the 6th visit after a reversal (Figure 4).

Chart, line chart

Description automatically generated

*Figure 4: Proportion of rewarded visits in the first 10 visits immediately after a reversal, indicated by the black circles and black line. Data were from experimental nights 2 and 3, after the bats’ choice behaviour stopped changing as an effect of reversal experience. Shading shows 95% confidence intervals*

# Discussion

In our experiment temporarily captive wild nectar-feeding bats participated in a spatial serial reversal learning task with two options that repeatedly alternated their rewarding properties. We examined whether nectar-feeding bats show improvement on this task, indicative of behavioural flexibility in a dynamically changing foraging environment. We found that the bats did switch to the newly-rewarding option from a previously-rewarding one with a decreasing number of perseverative visits, namely visits to the previously rewarding flower, with each successive experience of a reversal. This ‘speed of switching’ increased with five experiences of a reversal until it reached a plateau, and no further increase was seen as an effect of reversals on the later nights of the experiment(see Supplementary Material, figure S5). The bats did not reach the theoretically optimum performance of one error per reversal, but by the end of the first night they made significantly more than 50% of their visits to the rewarding flower by the 6th trial after the reversal (Figure 4). Perseverative visits were not necessarily ‘errors’: the bats were not given information as to whether the sudden lack of reward at a hitherto rewarding flower was temporary or not. A few persistent visits to the previously-rewarding flower might have been to make sure, as it were, of the new rewarding contingencies of the flowers, especially as there were a small number of wrongly unrewarded visits made to flowers that were programmed to give a reward. Potentially, a protocol with more noise built into the signal – say, one option yielding no reward and the other yielding a reward less than 100% of the time – might slow down the speed with which the bats switch to the rewarding option after the reversal.

Over a series of only five reversals there were significant changes in the bats’ decision-making behaviour. In order to quantify the “swiftness” of the change of the bats’ choices from one option to another we analyzed the effect of reversal, bins of 10 visits within each reversal block, and their interaction on the proportion of rewarded visits (Figure 4). This analysis revealed that as the bats experienced more reversals, the number of visits to the rewarding flower immediately after the reversal increased significantly. This proportion of rewarded visits was very high by the 20th visit of a reversal block, and so showed no further increase as an effect of reversal in the second half of the reversal block. The first reversal was experienced after a long series of trials with fixed reward contingencies (the bats experienced an alternation of reward contingencies during the training phase of the experiment, but this occurred with every single rewarded visit they made). Thus, in the first ten visits after the first reversal, the proportion of visits to the rewarding flower was the lowest value observed (Figure 2). Even excluding this first reversal block the bats switched to the rewarding flower faster as they experienced more reversals (see Supplementary Material).This is consistent with the findings of Stich (2004a, 2004b), where bats were trained with a set of 32 feeders as reward locations, which then alternated with a second set of 32 feeders at different spatial locations. The first set became unrewarding, and the second set became rewarding. This reversal resulted in a drop in performance, i.e., rewarded visits, indicating that the bats strongly rely on spatial memory to find food sources.

A methodological point that could have affected the behaviour of the bats is that the bats in this experiment received a rather large magnitude of reward each trial: 40 L in addition to the supplementary food that was always available.As the experiment went on, and the bats received several hundred of these large rewards, it is possible that they both became physically satiated, and learned that the environment was a rich one where food was easily obtained. One might expect therefore that motivation to find food, or to discriminate in favour of the richer source, decreased over the course of each night due to these reasons, with the animals relatively hungry at the beginning of their nightly foraging bout. However, this potential decrease in motivation did not seem to affect the number of visits before the switch even after the last reversal of the night: the bats switched to the rewarding flower within fewer visits after the fifth reversal than the fourth.

After the bats experienced no reward at a hitherto-rewarding option for the first time, the proportion of rewarded visits decreased, and never again became as high as it was in the first block. Bats, like all mammals studied, are known to adjust their choice behaviour between different available options according to their history of reinforcement at those options (Nachev and Winter 2012). If it is solely reinforcement history that dictates choice behaviour, then as the experience of reinforcement accumulates at both flowers over the course of the night, it is more difficult to discriminate which flower has a richer history. One would then expect that the bats’ behaviour approaches random choice as the night goes on, i.e., the Proprew would approach 0.5. Even if the animals do not rely on their entire history of reinforcement at an option for their decision-making but merely a part of it, one would expect to see a slower switch to the rewarding option following each reversal, and then a steady increase in rewarded visits. The exact opposite of both these outcomes was seen: the bats switched to the rewarding option after increasingly fewer choices.

While it is clear, therefore, that the bats’ choice behaviour was not dictated by the cumulative reinforcement history at the two options, it is also evident that the readiness to switch to the rewarding option had reached a maximum by the end of the first night, after experiencing five reversals. Although the optimum behaviour of one error per reversal is approached, it was not reached. As the speed of switching reached a plateau, the bats made about 5 visits to the previously-rewarding option in the first bin of 10 visits immediately after a reversal. In fact, less than total absorption to one source is to be expected if behaviour is capable to track potential changes in the rules of the environment. For instance, a bat could not know whether an even richer source could have become available, hence some small level of environmental sampling is probably adaptive.

The performance on the serial reversal task of animals that share similarities with bats in their foraging ecology is illuminating. Bumblebees in a serial reversal task like ours, with a large number of trials, showed a decrease in their perseverative errors, i.e., the errors immediately after a reversal, and an overall decrease in visits to the non-rewarding option as they experienced more reversals (Strang and Sherry 2014). The trial number seems to influence whether bees improve on the task: honeybees show generalization, making 50% of their choices to either option at the end of a serial reversal task with five trials between reversals (Menzel 1969; Mota and Giurfa 2010) and bumblebees show a decrease in the errors made after hundreds of trials (Chittka, 1998). The bats in our experiment showed far more rapid learning (Figure 2a, Figure 3b). When animals experience training on a reversal task beyond a certain high criterion of accuracy, a phenomenon called the overtraining reversal effect (ORE) has been seen in many cases: such “over-trained” animals show reversal within fewer trials than animals that have only been trained to the criterion (Reid 1953). The phenomenon has been observed in many species, including rats (Mackintosh 1965; Racht-Delatour and El Massioui 2000; Dhawan, Tait, and Brown 2019), pigeons (Williams 1967), rabbits (Orona et al. 1982), and even human children (Eimas 1966). The ORE may have contributed to the behaviour of the bats in our study: they were almost certainly overtrained as our experiment was non-probabilistic and every visit to the rewarding flower yielded a reward. However, our experiment was not intended to specifically test for this and lacked both a pre-set criterion and a control group that did not experience over-training.

Bumblebees also showed a small increase in the non-rewarded visits in the trials following the last two reversals in a serial reversal task with a large number of trials (Strang and Sherry 2014). This was interpreted as indicative of proactive interference, which occurs when previously-learned information interferes with the learning or remembering new information (Tello-Ramos et al. 2019). The bumblebees show a faster switch to the rewarding option after reversals like the bats in our experiment, and this improvement stops after about four reversals. Corvids show a similar saturation after five reversals on both colour and spatial serial reversal tasks (Bond, Kamil , and Balda 2007). Pigeons continue to show an increase in the proportion of rewarded visits up to about 10 - 15 reversals (Diekamp, Prior, and Güntürkün 1997). Great tits show performance similar to pigeons, with an overall proportion of rewarded visits below 0.6 but increasing up to 18 reversals. Marmosets show some of the fastest improvement of any animals on this task, making almost no perseverative errors after experiencing only two reversals (Clarke, Robbins, and Roberts 2008). Guppies show worse performance than most other animals tested with the serial reversal protocol, making a decreasing number of visits to the rewarding option as they experience up to ten reversals.

Several animals that rely strongly on spatial memory have also been studied in reversal learning tasks, particularly birds that cache food at various locations that they must remember and return to. Birds that are known to have better or more long-lasting spatial memory such as black-capped chickadees (Hampton, Shettleworth, and Westwood 1998), Clark’s nutcrackers (Lewis and Kamil 2006) and high elevation mountain chickadees (Croston et al. 2017) were worse at adapting to the new contingency after a reversal than the initial learning (reviewed in Tello-Ramos et al. 2019). This is expected for subjects with a reliance on spatial memory. Female shiny cowbirds (a brood parasitic species) have better spatial memory than the males (Guigueno et al 2014; Guigueno, MacDougall-Shackleton and Sherry 2016) to remember the location of multiple host nests. The females show a faster reversal than the males on a visual reversal task, but there was no difference between the sexes on a spatial task, where rapid learning was seen (Lois-Milevicich 2021). These data are consistent with the idea that there is a trade-off between acquiring new memories and retaining old ones, i.e., that proactive interference may be occurring in spatial reversal tasks, just like in bumblebees. It is known that Glossophagine bats have excellent spatial memory, potentially lasting up to several weeks (Stich 2004a; Stich 2004b; Winter and Stich 2005; Rose et al. 2016), but there was no evidence of proactive interference in the bats’ performance on the serial reversal task. At best there was a small variance increase in the choice behaviour on the first night after many reversals (Figure 2) had been experienced, for which there may be other explanations, such as satiety.

Our results are consistent with previous work of the same species of bat under natural conditions in the same environment (La Selva Biological Field Station, Costa Rica, Thiele 2006). This study, using the serial reversal task, evaluated the behavioural flexibility of nectar-feeding bats to fluctuations in food resource availability. Free-flying, ID-tagged wild bats interacted with 50 ID-sensor equipped artificial flowers placed over a 100 x 100 m area in the open forest that varied in their rate of nectar production. The allocation of flower types to spatial locations changed with the same pattern every night. During each night, bats adapted to the changes in resource availability. However, the bats needed four nights before they had adapted to the underlying recurring, predictable pattern of resource variability.

In most cases under natural foraging conditions, flowers are emptied in a single visit. There are however certain plants such as species of *Agave* or *Vriesea*, that may hold large amounts of nectar, which if undetected for a long time may require multiple hovering visits to deplete – “jackpot” rewards in other words. Thus, the ability to swiftly inhibit visiting a flower that had been rewarding for multiple visits is likely part of the bats’ natural foraging ecology as nectar-feeding animals: balancing the relative costs of making perseverative visits to ensure a flower is really empty, and the risk of foregoing a visit when there may still be nectar available in the flower.

What performance on the serial reversal task says about the cognitive mechanisms at work is not completely settled. The reversal learning task was once thought to primarily measure animals’ ability to exert inhibitory over their behavioural responses (Jones and Mishkin 1972), but Izquierdo et al. (2017) argue, based on more recent evidence that reversal learning experiments in general test animals’ ability to learn from the presence or absence of reward, estimate the likelihood of the occurrence of a reversal, and understand the task or option space. Any variation of the reversal learning task requires an animal to flexibly adjust its behaviour in response to the changing stimulus-reward associations. There is some evidence that these task demands are indicative of behavioural flexibility, as distinct from cognitive flexibility. Tait et al. (2018) argue that cognitive flexibility cannot be directly observed, but instead is inferred through the observation of behavioural flexibility in the reversal learning task. Rats that showed evidence of the ORE when a reversal was done between stimuli of a particular sensory modality also made more errors on a novel discrimination task that used stimuli of a different sensory modality (Dhawan, Tait, and Brown 2019). The authors of this study argue that this indicates that cognitive and behavioural flexibility can be dissociated, and the reversal learning paradigm is a test of the latter and not the former. Our study with nectar-feeding bats yielded strong evidence of a high capacity for behavioural flexibility, if not cognitive flexibility, evolved in the bats through a foraging ecology dominated by the search for nectar-rich flowers.

## Acknowledgements

We thank Alexej Schatz for the programming of the experimental software. We thank the members of the Winter lab for many useful discussions and our colleagues at La Selva Biological Field Station for all their support. We also thank \_\_\_ for their comments and suggestions for the improvement of the manuscript.

## Author Contributions

**SC**: formal analysis, data curation, writing – original draft, writing – review and editing. **SW**: conceptualization, experimental methodology, data collection. **AK**: formal analysis, writing – review and editing, supervision. **YW**: conceptualization, experimental methodology, resources, formal analysis, writing – review and editing, supervision. **VN**: formal analysis, data curation, writing – review and editing, supervision.

## Funding

Open Access funding enabled by: will have to see if there is any…

## Availability of data and code

All data and code are available in the Zenodo repository …

# Declarations

## Funding

This work was funded partly by a scholarship from the Deutscher Akademischer Austauschdienst (DAAD) to SC. Support was provided by EXC ….. and EXC ….. [need to look up the two project numbers]

## Conflict of interest

None

## Code availability

All data and code are available in the Zenodo repository …

# Electronic Supplementary Material

## Visits and approaches to the non-assigned flowers

Chart, timeline

Description automatically generatedOnly two out of the array of eight flowers were assigned uniquely to each bat but all the flowers were accessible to all the animals. The number of approaches to and attempts to get a reward from all the flowers, both assigned and not assigned, is shown in Figure 9.

Figure S1: Visits made by the bats to all the flowers, including the ones that were not assigned to them. Yellow bars are nose-pokes at the assigned flowers, where the bats attempted to get a reward by breaking the light-barrier. Purple bars are ‘fly-by’ events near the assigned flowers where the bat flew near the flower but did not attempt to get a reward. Orange bars are nose-pokes at the non-assigned flowers and black bars are fly-bys at the non-assigned flowers.

The number of approaches or attempts to get a reward at the non-assigned flowers was a small proportion of the overall number of approaches and reward-attempts at the flowers, less than 10% every night on average as Figure 10 shows.

*Chart, scatter chart

Description automatically generatedFigure S2: Proportion of visits or approaches to the un-assigned flowers out of the total number of visits or approaches to flowers. Coloured points are data from individual bats. Black points are the mean proportion per night and the error bars are 89% CIs.*

## Details of the statistical analyses

Weakly informative priors were used for the GLMMs in brms. All the models were estimated using 4 chains with a thinning interval of 3, with 1500 warm-up samples and 3000 post-warm-up samples for all the models except the one fitted to the data from the second and third nights, which had 1000 warm-up samples and 3000 post-warm-up samples. The response variable was the proportion of visits to the rewarding option, and a bernoulli likelihood function was used. For the model of the first experimental night, the reversal number, 10-visit bin within each block, and their interaction were the fixed effects. Slopes and intercepts were allowed to vary for each animal. For the model of the second and third experimental nights, the experimental night, reversal number, 10-visit bin within each block, night-reversal interaction and reversal-bin interaction were the fixed effects. Slopes and intercepts were allowed to vary for each animal.

Visual inspection of the trace plots, the effective sample size, the Gelman-Rubin convergence diagnostic () and the calculation of posterior predictions for the same clusters were all used to assess the fit of the models. In all the models the was equal to 1 for all the chains.

## The effect of reversal is not driven solely by the effect of the first reversal on the first night

Chart

Description automatically generatedThe effect of reversal on the visits to the rewarding flower persisted even when the data from the first block after the reversal were removed from the analysis, and a similar GLMM was fit (Figure S3). This analysis was done to ensure that the effect of multiple reversals on the proportion of rewarded visits was not solely due to the very first reversal, after which the proportion of rewarded visits was the lowest.

**b)**

**a)**

*Chart

Description automatically generated with medium confidence*

*Figure S3: a) Forest plot of the regression coefficients from the model of the effect of reversal and 10-visit bin on the visits to the rewarding flower, excluding the first reversal. Circles represent the means of the posterior distributions of the slope coefficients, thick horizontal lines represent 50% credible intervals, and thin horizontal lines 89% credible intervals. The numbers in bold are the means of the posterior distributions and 89% credible intervals b) Conditional effects plot from the model of the effect of reversal and 10-visit bin on the visits to the rewarding flower - excluding the first reversal - showing the two-way interaction between reversal and bin, sampling from the posterior distribution.*

## The proportion of rewarded visits does not increase due to reversal experience in the later stages of the experiment

At the very start of the second and third nights, in the first bin of visits before any experience of a reversal on that night, the average Proprew of all the bats was 69.8% [95% CI 64.3, 75], about 7 out of the 10 visits. This was significantly higher than random choice and higher than the Proprew in the corresponding bin of the first night. Indeed, over all the blocks on these two nights, the bats made significantly more than 50% of their visits to the rewarding flower within 6.67 visits [95% CI 5.42, 7.92] on average. After the first reversal on these nights the Proprew showed a similar pattern to the first night: a decrease immediately after the reversal and then an increase to near 100%: 94.8% [95% CI 94, 95.6], slightly higher than the 93% [95% CI 91.8, 94.1] Proprew on the first night.

Table

Description automatically generatedA GLMM similar to the ones fit to the data from the first night was fit to the data from the second and third nights. Excluding this first block, there was no effect of reversal on the Proprew, although there was a strong effect of 10-visit bin within each block. That is, the proportion of visits to the rewarded flower only increased within each block as the block progressed (Figures S4 and S5).

*Figure S4: Visits to the rewarding one of two options over second and third experimental nights. Data are average proportions for bins of ten visits averaged over all the individuals that made visits in each bin. Numbers indicate the bats that participated in a block. Shading shows 95% confidence intervals. Dashed lines show reversals.*

*Graphical user interface, chart, application, table, Excel

Description automatically generatedChart

Description automatically generated*

**b)**

**a)**

*Figure S5: a) Forest plot of the regression coefficients from a model of the effect of experimental night, reversal and 10-visit bin on the visits to the rewarding flower, excluding the first night. Circles represent the means of the posterior distributions of the slope coefficients, thick horizontal lines represent 50% credible intervals, and thin horizontal lines 89% credible intervals. The numbers in bold are the means of the posterior distributions and 89% credible intervals b) Conditional effects plot from the model of the effect of experimental night, reversal and 10-visit bin on the visits to the rewarding flower - excluding the first night - showing the two-way interaction between reversal and bin, sampling from the posterior distribution.*

# References

Audet, Jean-Nicolas, and Louis Lefebvre. 2017. “What’s Flexible in Behavioral Flexibility?” *Behavioral Ecology* 28 (4): 943–47. <https://doi.org/10.1093/beheco/arx007>.

Baker, Herbert G., Irene Baker, and Scott A. Hodges. 1998. “Sugar Composition of Nectars and Fruits Consumed by Birds and Bats in the Tropics and Subtropics.” *Biotropica* 30 (4): 559–86. <https://doi.org/10.1111/j.1744-7429.1998.tb00097.x>.

Balsters, Joshua H., and Narender Ramnani. 2011. “Cerebellar Plasticity and the Automation of First-Order Rules.” *Journal of Neuroscience* 31 (6): 2305–12. [https://doi.org/10.1523/JNEUROSCI.4358-10.2011.`](https://doi.org/10.1523/JNEUROSCI.4358-10.2011.%60)

Bond, Alan B., Alan C. Kamil, and Russell P. Balda. 2007. “Serial Reversal Learning and the Evolution of Behavioral Flexibility in Three Species of North American Corvids (*Gymnorhinus cyanocephalus, Nucifraga columbiana, Aphelocoma californica*).” *Journal of Comparative Psychology* 121 (4): 372–79. <https://doi.org/10.1037/0735-7036.121.4.372>.

Bürkner, Paul-Christian. 2017. “Brms: An *R* Package for Bayesian Multilevel Models Using *Stan*.” *Journal of Statistical Software* 80 (1): 1–28. <https://doi.org/10.18637/jss.v080.i01>.

Carpenter, Bob, Andrew Gelman, Matthew D. Hoffman, Daniel Lee, Ben Goodrich, Michael Betancourt, Marcus Brubaker, Jiqiang Guo, Peter Li, and Allen Riddell. 2017. "*Stan*: A probabilistic programming language." *Journal of Statistical Software* 76 (1): 1–32. <https://www.osti.gov/servlets/purl/1430202>

Chittka, Lars. 1998. “Sensorimotor learning in bumblebees: long-term retention and reversal training.” *The Journal of experimental biology*, 201(4): 515-524. <https://doi.org/10.1242/jeb.201.4.515>

Clarke, Hannah F., Trevor W. Robbins, and Angela C. Roberts. "Lesions of the medial striatum in monkeys produce perseverative impairments during reversal learning similar to those produced by lesions of the orbitofrontal cortex." 2008. *Journal of Neuroscience* 28(43): 10972-10982. https://doi.org/10.1523/JNEUROSCI.1521-08.2008

Croston, Rebecca, Carrie L. Branch, Angela M. Pitera, Dovid Y. Kozlovsky, Eli S. Bridge, Thomas L. Parchman, and Vladimir V. Pravosudov. 2017. "Predictably harsh environment is associated with reduced cognitive flexibility in wild food-caching mountain chickadees." *Animal Behaviour* 123: 139-149. <https://doi.org/10.1016/j.anbehav.2016.10.004>

Dhawan, Sandeep S., David S. Tait, and Verity J. Brown. 2019. “More Rapid Reversal Learning Following Overtraining in the Rat Is Evidence That Behavioural and Cognitive Flexibility Are Dissociable.” *Behavioural Brain Research* 363: 45–52. <https://doi.org/10.1016/j.bbr.2019.01.055>.

Diekamp, Bettina, Helmut Prior, and Onur Güntürkün. 1994. "Functional lateralization, interhemispheric transfer and position bias in serial reversal learning in pigeons (Columba livia)." *Animal Cognition* 2(4): 187-196.

Eimas, Peter D. 1966. "Effects of overtraining, irrelevant stimuli, and training task on reversal discrimination learning in children." *Journal of Experimental Child Psychology* 3 (4):315-323. <https://doi.org/10.1016/0022-0965(66)90075-0>

Hampton, Robert R., Sara J. Shettleworth, and Richard P. Westwood. 1998."Proactive interference, recency, and associative strength: Comparisons of black-capped chickadees and dark-eyed juncos." *Animal Learning & Behavior* 26 (4): 475-485. <https://doi.org/10.3758/BF03199241>

Guigueno, Mélanie F., Danielle A. Snow, Scott A. MacDougall-Shackleton, David F. Sherry. 2014. “Female cowbirds have more accurate spatial memory than males.” *Biology Letters*, 10(2): 20140026. <https://doi.org/10.1098/rsbl.2014.0026>

Guigueno, Mélanie F., Scott A. MacDougall-Shackleton, David F. Sherry. 2016. Sex and seasonal differences in hippocampal volume and neurogenesis in brood-parasitic brown- headed cowbirds (*Molothrus ater*). *Developmental Neurobiology*, 76(11): 275-1290. https://doi.org/ 10.1002/dneu.22421.

Harrell Jr., Frank, E., 2021. Hmisc: Harrell Miscellaneous. R package version 4.6-0. <https://CRAN.R-project.org/package=Hmisc>

Izquierdo, Alicia, Jonathan L. Brigman, Anna K. Radke, Peter H. Rudebeck, and Andrew Holmes. 2017. “The Neural Basis of Reversal Learning: An Updated Perspective.” *Neuroscience* 345 (March): 12–26. <https://doi.org/10.1016/j.neuroscience.2016.03.021>.

Jones, B. and M. Mishkin. 1972. “Limbic lesions and the problem of stimulus—reinforcement associations.” *Experimental neurology*, 36 (2): 362-377. [https://doi.org/10.1016/0014-4886(72)90030-1](https://doi.org/10.1016/0014-4886(72)90030-1" \o "Persistent link using digital object identifier" \t "_blank)

Lewis, Jody L., and Alan C. Kamil. 2006. "Interference effects in the memory for serially presented locations in Clark's nutcrackers, *Nucifraga columbiana*." *Journal of Experimental Psychology: Animal Behavior Processes* 32 (4): 407. [https://doi.org/10.1037/0097-7403.32.4.407](https://psycnet.apa.org/doi/10.1037/0097-7403.32.4.407)

Lois-Milevicich, Jemina, Mariano Cerrutti, Alex Kacelnik, and Juan C. Reboreda. 2021. “Sex differences in learning flexibility in an avian brood parasite, the shiny cowbird.” *Behavioural Processes* (189): 104438. <https://doi.org/10.1016/j.beproc.2021.104438>

Mackintosh, Nicholas. J. 1965. “Overtraining, reversal, and extinction in rats and chicks.” *Journal of Comparative and Physiological Psychology*, 59(1): 31. [https://doi.org/10.1037/h0021620](https://psycnet.apa.org/doi/10.1037/h0021620)

McElreath, Richard. 2020. “Statistical Rethinking: A Bayesian Course with Examples in R and Stan.” Chapter 4. 2nd ed. Boca Raton: Chapman; Hall/CRC. <https://doi.org/10.1201/9780429029608>.

Menzel, Randolf. 1968. “Das gedächtnis der honigbiene für spektralfarben.” *Zeitschrift für vergleichende Physiologie*, 60(1): 82-102.

Mota, Theo, and Martin Giurfa. 2010. "Multiple reversal olfactory learning in honeybees." *Frontiers in behavioral neuroscience* 4: 48. <https://doi.org/10.3389/fnbeh.2010.00048>

Nachev, Vladislav, Kai Petra Stich, and York Winter. 2012. “Weber’s law, the magnitude effect and discrimination of sugar concentrations in nectar-feeding animals.” *PloS one* 8 (9): e74144. <https://doi.org/10.1371/journal.pone.0074144>

Nachev, Vladislav, Kai Petra Stich, Clemens Winter, Alan Bond, Alan Kamil, and York Winter. 2017. “Cognition-Mediated Evolution of Low-Quality Floral Nectars.” *Science* 355 (6320): 75–78. <https://doi.org/10.1126/science.aah4219>.

Nachev, Vladislav, and York Winter. 2012. “The Psychophysics of Uneconomical Choice: Non-Linear Reward Evaluation by a Nectar Feeder.” *Animal Cognition* 15 (3): 393–400. <https://doi.org/10.1007/s10071-011-0465-7>.

Ohashi, Kazuharu, and James D. Thomson. 2005. “Efficient harvesting of renewing resources.” *Behavioral Ecology* 16 (3):592-605. <https://doi.org/10.1093/beheco/ari031>

Orona, Edward, Kent Foster, Richard W. Lambert, and Michael Gabriel. 1982. "Cingulate cortical and anterior thalamic neuronal correlates of the overtraining reversal effect in rabbits." *Behavioural Brain Research* 4(2): 133-154. <https://doi.org/10.1016/0166-4328(82)90069-9>

R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.

Reid, Lyne S. 1953. "The development of noncontinuity behaviour through continuity learning." *Journal of experimental psychology* 46(2): 107. [https://doi.org/10.1037/h0062488](https://psycnet.apa.org/doi/10.1037/h0062488)

Rose, Andreas, Miriam Kolar, Marco Tschapka, and Mirjam Knörnschild. 2016. "Learning where to feed: the use of social information in flower-visiting Pallas’ long-tongued bats (*Glossophaga soricina*)." *Animal cognition* 19 (2): 251-262. <https://doi.org/10.1007/s10071-015-0930-9>

Shettleworth, Sara J. 2010. “Cognition and the Study of Behavior.” Chapter 1 in: “Cognition, Evolution, and Behavior.” 2nd ed. Oxford; New York: Oxford University Press. <http://www.dawsonera.com/depp/reader/protected/external/AbstractView/S9780199717811>.

Stich, Kai-Petra. 2004a. “Nahrungssuche innerhalb kleinräumiger Blütenansammlungen I: Langzeit- Ortsgedächtnisfähigkeiten der Blütenfledermaus *Glossophaga soricina.*” Chapter 2 in: “Ortsgedächtnis für Blütenpositionen bei der Blütenfledermaus *Glossophaga soricina.*” Dissertation. Ludwig-Maximilians-Universität, Munich, Germany. https://edoc.ub.uni-muenchen.de/2008/1/Stich\_Kai\_Petra.pdf

Stich, Kai-Petra. 2004a. “Nahrungssuche innerhalb kleinräumiger Blütenansammlungen II: Bewegungsregeln oder räumliches Arbeitsgedächtnis?” Chapter 2 in: “Ortsgedächtnis für Blütenpositionen bei der Blütenfledermaus *Glossophaga soricina.*” Dissertation. Ludwig-Maximilians-Universität, Munich, Germany. <https://edoc.ub.uni-muenchen.de/2008/1/Stich_Kai_Petra.pdf>

Strang, Caroline G., and David F. Sherry. 2014. “Serial Reversal Learning in Bumblebees (*Bombus impatiens*).” *Animal Cognition* 17 (3): 723–34. <https://doi.org/10.1007/s10071-013-0704-1>.

Tait, David S., Eric M. Bowman, Lorenz S. Neuwirth, and Verity J. Brown. 2018. “Assessment of Intradimensional/Extradimensional Attentional Set-Shifting in Rats.” *Neuroscience & Biobehavioral Reviews* 89: 72–84. <https://doi.org/10.1016/j.neubiorev.2018.02.013>.

Tello-Ramos, Maria C., Carrie L. Branch, Dovid Y. Kozlovsky, Angela M. Pitera, and Vladimir V. Pravosudov. 2019. “Spatial Memory and Cognitive Flexibility Trade-Offs: To Be or Not to Be Flexible, That Is the Question.” *Animal Behaviour* 147: 129–36. <https://doi.org/10.1016/j.anbehav.2018.02.019>.

Thiele, Johannes. 2006. “Erlernen lokaler Ressourcenverteilungen durch Blumenfledermäuse an einem Blütenfeld aus künstlichen Blüten im Freiland.” Chapter 4 in:“ “Nahrungssuchstrategien der nektarivoren Fledermaus *Glossophaga commissarisi* (Phyllostomidae) im Freiland - eine individuenbasierte Verhaltensstudie unter Verwendung von Transpondertechnik.” Dissertation. Ludwig-Maximilians-Universität, Munich, Germany. <https://edoc.ub.uni-muenchen.de/5566/1/Thiele_Johannes.pdf>

Thiele, Johannes, and York Winter. 2005. “Hierarchical Strategy for Relocating Food Targets in Flower Bats: Spatial Memory Versus Cue-Directed Search.” *Animal Behaviour* 69 (2): 315–27. <https://doi.org/10.1016/j.anbehav.2004.05.012>.

Tschapka, Marco. 2004. "Energy density patterns of nectar resources permit coexistence within a guild of Neotropical flower-visiting bats." *Journal of Zoology* 263 (1): 7-21. <https://doi.org/10.1017/S0952836903004734>.

Tölch, Ulf, and York Winter. 2007. “Psychometric Function for Nectar Volume Perception of a Flower-Visiting Bat.” *Journal of Comparative Physiology A* 193 (2): 265–69. <https://doi.org/10.1007/s00359-006-0189-3>.

van Golf Racht‐Delatour, Barbara, and Massioui, Nicole E. 2000. Alleviation of overtraining reversal effect by transient inactivation of the dorsal striatum. *European Journal of Neuroscience*, 12(9): 3343-3350. [**https://doi.org/10.1046/j.1460-9568.2000.00192.x**](https://doi.org/10.1046/j.1460-9568.2000.00192.x)

von Helversen, Otto, L., Winkler, and H.J. Bestmann. 2000. “Sulphur-Containing ‘Perfumes’ Attract Flower-Visiting Bats.” *Journal of Comparative Physiology A* 186 (2): 143–53. <https://doi.org/10.1007/s003590050014>.

Williams, D. I. 1967. “The overtraining reversal effect in the pigeon.” *Psychonomic Science*, 7(7): 261-262. https://doi.org/10.3758/BF03331106

Winter, York, Sophie von Merten, and Hans-Ulrich Kleindienst. 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(2): 283-290. <https://doi.org/10.1016/j.jneumeth.2004.07.002>

Winter, York, and Kai Petra Stich. 2005. “Foraging in a Complex Naturalistic Environment: Capacity of Spatial Working Memory in Flower Bats.” *Journal of Experimental Biology* 208 (3): 539–48. <https://doi.org/10.1242/jeb.01416>.