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Time budget and courtship costs in male spotted bowerbirds: A GPS-based comparison between breeding and non-breeding seasons

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Contents:

Abstract

Sexual selection has been studied for a long time, but it is still not fully understood. This is particularly the case when looking at the relation between costs of sexual traits and their benefits. In this study, I investigated the costs of courtship in spotted bowerbirds (*Chlamydera maculata*), looking at time budget differences between seasons. Furthermore, I did a vegetation survey to understand what foraging sites they are attracted to. Spotted bowerbirds build structures called bowers that are used by the male as a stage to perform courtship displays towards females. The construction and the maintenance of this structure as well as the practice of the courtship is time intensive. However, the cost of a behaviour is meaningful only if it causes the individual to make a trade off with another behaviour. Thus, I aimed to show if significant differences in the time budgets of the males between the breeding season and non-breeding season could be found. I used a combination of camera traps and GPS tracking to assess time budgets and compared them across seasons. Comparing the two methods revealed no correlation. Furthermore, no correlation between mating success and time investment into the bower was found. When the birds are foraging, they look for sites that are close to their bower and show a high coverage of plants of interest. The GPS data showed that males spend significantly less time at the bower in the non-breeding season than during the courtship season, suggesting that differences in the time budgets between breeding and non-breeding season exist. These results suggest that courtship behaviours are indeed costly for the individual, at least in the aspect of time budget.

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Introduction

"Sexual selection is any [natural] selection that arises from fitness differences associated with non-random success in the competition for access to gametes for fertilization." (Shuker & Kvarnemo, 2021). This definition is one of the most recent descriptions to the "sexual selection theory", which was first introduced in 1871 by Charles Darwin in his book *The Descent of Man and Selection in Relation to Sex*. This theory aimed to explain the occurrence of sexually dimorphic phenotypic traits such as stag antlers or bright plumage in male birds. According to Charles Darwin, such male morphological features have no functional value, except to attract females and therefore increase males' reproductive chances. Over the course of the past 150 years many researchers have worked on the topic and introduced various models to help understand and support the sexual selection theory. However, it is important to understand that sexual selection is a multilayered complex mechanism as it can be expressed in many ways. This was already acknowledged by Darwin, as he identified the two main mechanisms of sexual selection, namely intrasexual and intersexual selection (Darwin, 1871; Jones & Ratterman, 2009).

Intrasexual selection refers to the competition between individuals of the same sex. Commonly, two males compete in several possible ways, and the successful individual acquires reproductive success. Male-male competition can be found throughout the animal kingdom, ranging for example from mammals like the red deer, which use a big variety of sexual behaviours to determine who the strongest male is such as displaying their antlers (Peña *et al.*, 2024), to amphibians like the natterjack toads using vocalizations to signal their fitness to competing males (Arak, 1983). However, females also show individual preferences, and it is not always the outcome of such competition that predicts mating. Such preferences are known as mate-choice and can be defined as intersexual selection. In Darwin's times, the concept of intersexual selection was heavily criticized as it was believed for long that female animals could not have preferences for aesthetics. Accepting that females indeed have aesthetic preferences took over a century (Darwin, 1871; Jones & Ratterman, 2009). The acceptance of mate-choice led to the conclusion that „... males with the preferred trait will leave greater numbers of offspring, and their trait values will tend to increase in frequency in the population." (Jones & Ratterman, 2009).

A pioneer in the field of intersexual selection was R. A. Fisher who elaborated on Darwin's ideas and introduced the Fisherian runaway selection hypothesis (Fisher, 1915, 1930) to explain the evolution of exaggerated traits. Such traits are phenotypic traits that have been pushed beyond functional necessity through sexual selection (Andersson, 1994). He argued that the female preference for a male's trait and the trait itself co-evolve, leading to increasingly exaggerated features. Fisher identified three stages in the evolutive time of a secondary sexual trait. In the initial phase, a trait that is already favoured by natural selection becomes amplified and exaggerated through the pressures of sexual selection. In the following stage, the advantages this trait offered for survival diminish and can even disappear. However, the attractiveness of this trait for the selecting sex continues to strengthen, which explains its existence. This leads to a trade-off between the advantages the trait offers for reproduction and the associated costs for survival, eventually reaching an equilibrium. In the final stage, the advantages to sexual reproduction are outweighed by the costs of the trait which leads to a decay of the trait and of the preference for it in the opposite sex (Fisher, 1915, 1930).

The Fisherian runaway selection hypothesis is based on the existence of mate choice. Without a preference for certain phenotypic traits, those traits would not become exaggerated. With the role of female choice as a driver of sexual selection gaining acceptance, the evolution of mate choice became a topic of intensive research, leading to the emergence of more theoretical background.

In the direct benefit models, it is hypothesized that females choose males that offer them an immediate benefit, such as a nuptial gift. In bushcrickets (*Tettigonidae*) the females choose males that can provide the biggest spermatophores as nuptial gifts, which offer important nutrients (Gwynne, 1984). Other benefits can be good parental care, such as in fifteen-spined sticklebacks (*Spinachia spinachia*) where females prefer males with better parental care abilities (Östlund & Ahnesjö, 1998) or a higher-quality territory, that offers the best resources (Emlen & Oring, 1977). For example, female red-winged blackbirds choose an already mated male with a better nesting site over an unmated male with a worse nesting site, even though polygynous mating diminishes the females reproductive success (Pribil & Searcy, 2001). If there are no directly quantifiable benefits to offer other than fertilization, but only indirect benefits such as good genes, the mechanisms underlying female-choice are less apparent (Jones & Ratterman, 2009).

There are several different models aiming to explain indirect benefit mating systems. The two most established models are the Fisherian Model and the condition-dependent indicator model which is based on Zahavi's Handicap principle (Zahavi, 1975 but see Jones & Ratterman, 2009). The Fisherian model is based on the Fisherian runaway selection hypothesis (see above). Whilst for the Fisherian model only a specific ornament in one sex and a preference for this ornament in the opposite sex is needed, the condition-dependent indicator models add another component, which is a viability trait (Jones & Ratterman, 2009). With the handicap principle, Amit Zahavi suggested that sexual selection helps the choosing sex to select the highest quality mate (Zahavi, 1975). He argued that individuals evolve body ornaments that are detrimental to their survival to advertise their own fitness, because only individuals with sufficient fitness can sustain such body ornaments. A widely cited example are the elongated tail feathers of the peacock, which bear costs to the male (Zahavi, 1975). Both sexes benefit: the bearing sex in securing mates and the choosing sex in finding mates of higher quality. Such ornaments are associated with costs, which for example can be in the form of higher time investment into courtship behaviours, leading to a trade-off with other behaviours. Due to these involved costs, Zahavi argued that such advertisements of male quality are honest, and cheating is difficult (Zahavi, 1975). However, over time the theory has been criticised that extra costs do not necessarily lead to honest signalling especially when there is a conflict of interest between the sender and the receiver of the signal and deception would be advantageous (Penn & Számadó, 2020). Even though not all aspects are fully understood yet, indirect benefit models and direct benefit models provide a frame to study mate choice in relation to trait cost (Jones & Ratterman, 2009). An effective approach to research sexual selection and especially mate choice is to study courtship displays (Vijendravarma & Leopold, 2022).

Courtship displays can be defined as a collection of behaviours that are shown by an individual to attract and mate with an individual of the opposite sex. These displays can be extremely diverse and be performed on multiple sensory modalities simultaneously (Mitoyen *et al.*, 2019). However they also may implement costs upon the individual performing them in different forms, such as high energetic costs or a high time investment (Clark, 2012; Mowles & Jepson, 2015; Mitoyen *et al.*, 2019; Anderson *et al.*, 2024a). Most displays include two or more sensory modalities and signals that address separate sensory

systems in the receiving individual and are therefore called multisensory courtship displays. The components of the courtship can either appear sequentially, like in the ring-necked pheasant (*Phasanius colchicus),* where the courtship display is divided in a pre-choice period to attract the female into proximity and a lateral display when the female is in proximity (Mateos & Carranza, 1999), or simultaneously. Multisensory courtship displays can be found throughout the animal kingdom, especially in the family of songbirds, such as in the Cordon-bleus (*Uraeginthus spp.)*. The courtship includes both sexes performing "… multimodal courtship displays by holding a piece of nest material, bobbing up and down, and singing." (Ota, 2020). During the courtship display, males use secondary sexual traits such as bodily ornaments (Mitoyen *et al.*, 2019). This can range from bright plumage in Birds (Andersson, 1994) to tail lengths in sea-snakes *Laticauda colubrina* (Shine & Shetty, 2001). Moreover, non-bodily ornaments or extended phenotypes can also be used as sexual signals. In this context, the extended phenotype refers to traits or structures created by an organism that influence mate attraction or reproductive success, even though they are not part of the organism's body. As extended phenotypes are located in the environment, they are easily accessible and therefore measurable and manipulable for experiments (Dawkins, 1982). One of the most prominent but relatively understudied examples in the context of courtship is the bower of bowerbirds (Schaedelin & Taborsky, 2009).

Bowerbirds (*Ptilonorhynchidae*) are a family of birds which are endemic to Australia and New Guinea. Their unique courtship behaviours include the construction of a structure called the bower (Figure 1) that is used by the male as a stage to perform courtship displays towards females. They can have various shapes depending on the species and can reach up to two meters in diameter (Frith & Frith, 2004; Rowland, 2008). Furthermore, males decorate their bowers with various items of certain colours. For example, the spotted bowerbird (*Chlamydera maculata*), the species this study focuses on, preferentially collect white shells or bones and green berries of *Solanum* (Frith & Frith, 2004; Madden *et al.*, 2004a). It has been shown that the number and type of decorations correlate with the number of female visitations or with the males' mating success (Borgia, 1995; Madden, 2003). It has also been hypothesized that different decorations serve different functions. While the colourful decorations could keep females interested when they are at the

bower, the bones and other white decorations could be distributed around the bower to attract females to the bower by making it more visible from above (Borgia, 1995).

Figure 1: Picture of a spotted bowerbird's bower

Constructing a bower and maintaining it is time intensive, with building materials and decorations having to be gathered from the environment. After construction the individuals revisit their bower for maintenance and courtship displays. Additionally, birds must protect their bowers from rival bower owners who may steal decorations and destroy their bowers. These behaviours collectively reduce the time available for other activities such as foraging (Isden *et al.*, 2025). To evaluate how successful an individual is, the number of copulations can be used as a proxy for reproductive success (Madden, 2003). During the breeding season, bower owning male spotted bowerbirds spend approximately 50% of the day at their bower (Frith & Frith, 2004). One third of that time is dedicated to maintenance of their bower, whilst they spend 12% of that time displaying or practicing their display, and the remainder for other activities (Frith & Frith, 2004). Isden *et al.* (2025) found lower attendance time than Frith and Frith (2004) - probably because of the difference in their methods - but nonetheless substantial with values ranging from 2 to 6.5% of the total time filmed. They also hypothesized that bower attendance could be influenced by environmental factors such as rain, which also influences food availability. In moister seasons there are more resources available, therefore the individuals could need less time for foraging and could invest more time into the bower. This suggests

that bower attendance is influenced by resource availability. Ultimately, this time investment into the bower cannot be used for foraging activities. Therefore, the individuals have to choose how much time they want to allocate to courtship behaviours and foraging behaviours. This trade-off in the time budget can be seen as a proxy for the trade-off between survival and reproduction.

In the past, time budgets and bower activity were calculated through in person observations (Frith & Frith, 2004) or by using camera traps only (Isden *et al.*, 2025). This offers insights into the behaviours that are shown when the birds are present at their bowers during the breeding season. However, the behaviours shown when the birds are away from the bower and during the non-breeding season remain unknown. Therefore, possible trade-offs in the time allocation towards different behaviours during the breeding season are difficult to capture. To empirically investigate such trade-offs, the present study aims to compare the time budget of the males in the breeding season with their activities during the rest of the year. Male spotted bowerbirds have been reported to abandon their bowers during the non-breeding season (Frith & Frith, 2004). Recently it has been shown that revisitation numbers do not significantly change between seasons (Spezie *et al.*, 2025). However given that courtship displays only occur during the breeding season, the non-breeding season can be used as a control to quantify time budget changes in the breeding season (Frith & Frith, 2004).

In this study, I used a combination of videos recorded by motion-triggered camera traps at the bower, seven years of GPS tracking data and a botanical field survey to assess the existence of a trade-off between foraging and courtship in spotted bowerbirds. The cameras were placed at ten bowers by Job Knoester throughout the breeding season of 2024. Behavioural scoring of the video data was conducted to quantify in detail the males' time budget at their bowers. Job Knoester and Giovanni Spezie outfitted 10 bower owning male spotted bowerbirds with GPS tracking devices from 2018 onwards. To understand the behaviour of these birds when outside of the bowers I analysed the GPS data to determine locations that were visited by bowerbirds. During my field season in Taunton National Park (Scientific), Queensland, Australia, I visited these locations to identify resources of potential interest for the birds, such as food, bowers, and decorations. As bowerbirds spend a substantial portion of their time budget at the bowers during the breeding season (Borgia, 1995; Madden, 2003; Frith & Frith, 2004; Isden *et al.*, 2025), I hypothesize that a

trade-off between survival and reproduction can be found and therefore the time budgets of males differ significantly between the two seasons. Specifically, the increased investment in courtship behaviours is expected to reduce the time allocated to other essential activities, such as foraging. I expect that during the breeding season, a significant proportion of male bowerbirds' time budget is dedicated to the maintenance of their bower and courtship display, resulting in a trade-off with foraging. This indicates that courtship activities impose a substantial temporal cost on individual males.

Methods

Study site and data collection

The studied spotted bowerbird population inhabits the Taunton National Park (Scientific) in Queensland, Australia. This park was established in 1986 to protect the only wild living population of bridled nailtail wallabies *(Onychogalea fraenata)*. It is located in the northern brigalow belt bioregion and is therefore characterised by brigalow (*Acacia harpophylla*) forest. Other parts of the park show grassy eucalypt woodland, which is dominated mostly by poplar box *(Eucalyptus populnea*). These vegetation types were historically widespread throughout Queensland. Today most of the area has been cleared for cattle grazing. The soil in the park is either composed predominantly of clay, favouring brigalow forests or texture-contrast soils, the latter supporting the eucalyptus dominated areas. As Taunton National Park is at the level of the tropic of Capricorn, the climate is subtropical and droughts are frequent and present challenges for the wildlife population (Taunton National Park (Scientific) Management Plan, 2011).

The park is accessible only to scientists and hosts a population of spotted bowerbirds. This population has been studied since 1998 by Joah Madden and his colleagues (i.e. Madden, 2003; Madden *et al.*, 2004a, 2004b; Isden *et al.*, 2025), and since 2018 by our team (i.e. Spezie & Fusani, 2022; Knoester *et al.*, 2024). As a result of the previous work carried out on this population, a substantial proportion of the individuals are marked with a unique combination of colour bands, allowing their identification. Each combination consists of 5 plastic colour bands and a single metal band with a unique number provided by the Australian Bird and Bat banding Scheme (ABBBS). For that, mist nets were used to catch the birds at their bowers. (Knoester *et al.*, 2024; Spezie *et al.*, 2025). I conducted fieldwork at Taunton National Park (Scientific) from 18. September to 14. October and

from 11. November to 16. December 2025. In total 36 active bowers were located and monitored in the field season of 2025.

Ten bower-owning males were outfitted from 2018 to 2025 with the GPS loggers “GiPSy6” and “Remote” from TechnoSmArt Europe. Not all individuals wore GPS trackers for the same time and duration throughout this period, as it depended primarily on catching success. The Gipsy6 and Remote loggers have high sensitivity and are therefore suitable for use in wooded, or shrubby habitats. The devices are charged by small integrated solar panels and remotely send the GPS data to external devices, when the logger is in range. The loggers were set to record the bird’s location every hour during daylight hours, as long as they had enough battery and connection to satellites. The trackers were chosen in size specifically for the spotted Bowerbird never exceeding five percent of the individual’s bodyweight. They were placed on the upper back of the birds, with straps made of Teflon ribbon going around the shoulder-joints, being fixed in place with a metal clamping ring (Figure 2). This method proved to be harmless to the individuals over the past years (Lundblad *et al.*, 2024).

The Bowers were monitored through the entire field season using motion-activated camera traps (Browning Recon Force Advantage HD and Browning Recon Force Elite). They were mounted in front of one of the bower entrances on a wooden pole at a standardized distance of 175 cm from the bower centre. Cameras were set to record for at least 30 seconds upon motion detection. Video analyses were based on data gathered in the field season of 2024 (20. September – 15. December 2024).

Figure 2: picture of GPS backpack on male spotted bowerbird

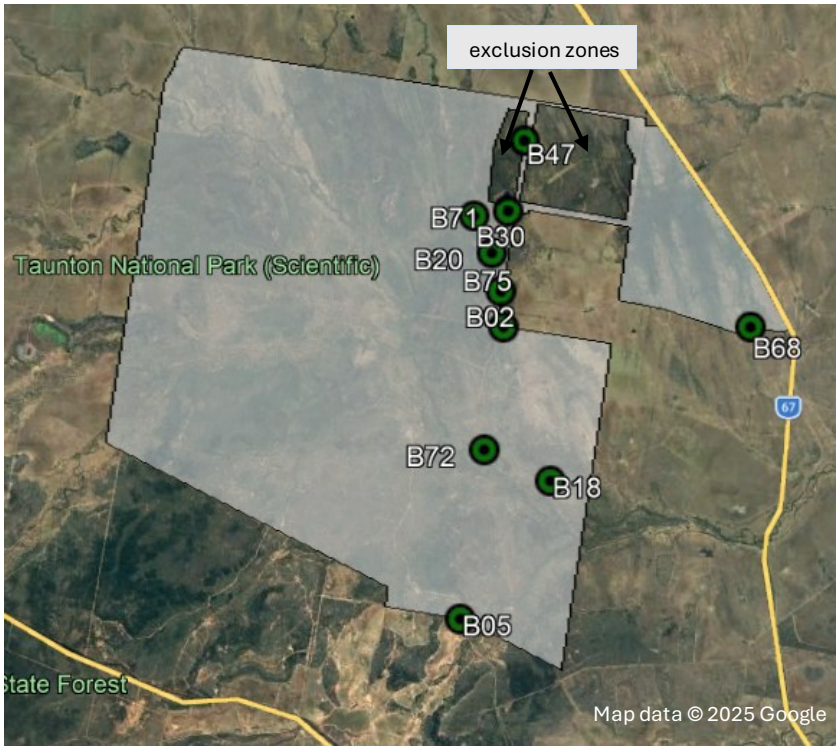

Figure 3: satellite picture with the bower locations and the limits of Taunton National Park. The black arrows mark the exclusion zones. The access to those zones of the park is prohibited. Map data © 2025 Google.

GPS data analyses for vegetation survey

A vegetation survey was conducted to determine what the birds are doing when they are away from the bower. To find the squares of interest for the vegetation survey, we analysed the GPS data in a GPS count cell analysis, with R (R Core Team, 2025). As a base framework to find the locations of interest a shapefile of the Taunton National Park was used. For the analyses a Lambert azimuthal projection was used *("+proj=laea*

+lon_0=149.2 +lat_0=-23.55 +datum=WGS84 +units=m +no_defs"). A matrix of squares of 10 m x 10 m in the same coordinate system as the national park shapefile was created and laid over the Taunton National Park (scientific). The size of the square was chosen based on the vegetation type found at the study site (Kent, 2012). The recorded GPS fixes of each individual were located and each point laying in one of the squares was recorded (Figure 4). All squares with at least one recorded GPS point were combined in a list. The coordinates were then transformed back into the standard coordinate system, for further investigation in the field. As visiting all squares in the field was impossible due to time restrictions 20 squares per individual were randomly chosen with probabilities weighted by the number of visits. This means a square that was visited more often, is more likely to be selected than a rarely visited square. The probability of a square to be selected was directly proportional to its visitation frequency. This approach was adopted because most of the squares have very few visits whilst only a few show high visitation numbers. This method ensured that squares of all visitation frequencies and not only squares with very few visitation rates were sampled.

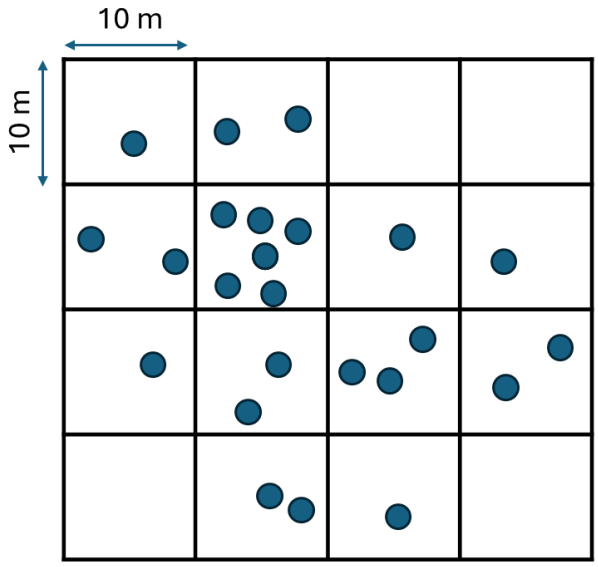

Figure 4: scheme of GPS cell points analyses

Vegetation survey

The GPS data analysis generated a list of selected squares for each individual. Each entry featured the square ID and the coordinates of the locations. To prevent any potential bias the frequency of visits was removed. In total I surveyed 220 squares. For each plot, I laid out sampling squares of 10 m x 10 m with measuring tape and metal pegs at the corners (Figure 5). I estimated the coverage for all plant species that were present in the selected

squares from the ground level all the way up to the canopy. As plant species could be overlaying at different heights, there was a possibility for the total coverage to be over 100 percent. The vegetation analysis focused on plants that are known to be of relevance for spotted bowerbirds (Table 1). The species list was compelled following Frith & Frith, 2004. Given that spotted bowerbirds are predominantly frugivorous, I was able to access if these sites are potentially foraging sites or not (Frith & Frith, 2004). Additionally, all plant species that are known to be used as decorations, such as *Solanum* berries were recorded (Frith & Frith, 2004; Madden *et al.*, 2004a). Other decoration types such as shells were recorded as well, but as they were rare, they won't be discussed further in this study. I visually estimated the coverage of the species, which inevitably leads to some approximations. However, since I was the only one doing the estimation of coverage these subjective inaccuracies should be consistent throughout the entire study.

Figure 5: example of a square for the vegetation analyses

Table 1: list of plants of interest (focal plants) for spotted Bowerbirds adapted from (Frith & Frith, 2004)

species	
Currant bush (*Carissa ovata)*	Willow acacia *(Acacia salicina)*
Brigalow (*Acacia harpophylla*)	Cork tree (*Hakea lorea*)
Wilga *(Geijera parviflora)*	*Senna sp.*
Turkey bush *(Eremophila deserti)*	Queensland Bluegrass *(Dichanthium sericeum)*
False Sandalwood *(Eremophila mitchellii)*	*Solanum sp.*
Dogwood *(Erythroxylum australe)*	Spotted emu bush *(Eremophila maculata)*
Northern sandalwood *(Santalum lanceolatum)*	Misteltoe *(Viscum sp.)*
Ruby saltbush (Enchylaena tomentosa)	Queensland ebony (*Diospyros humilis)*
Desert lime (Citrus Glauca)	Wild orange *(Capparis mitchellii)*
Desert Jasmine (Jasminum lineare)	Native orange *(Capparis lasiantha)*
Waterbush *(Myoporum acuminatum)*	

Video categorisation

I categorised the video recordings with the open-source software BORIS (Friard & Gamba, 2016), for which I designed a standardized protocol (see supplementary materials). There are three types of videos, false triggers, which show no spotted bowerbirds or spotted bowerbird vocalizations and no other species of animals. Those were categorized with the behaviour "delete". Videos showing no bowerbird, but any other animal species were categorized by the behaviour "animal". If there were bowerbirds present in the video, the subjects present were identified with the help of their colour bandings (Figure 6). In the case that the subjects didn't have any colour bandings or the banding was unidentifiable, the subjects were recorded as "unidentified". Having identified the subjects, their shown behaviours were determined. Behaviours include "maintenance", which is defined as constructing and decorating their bower, or "display with other(s)", which means doing courtship display with other individuals present. The full list of behaviours is available in Table 2. The behaviours from row 7 to 14 were combined as the behaviour "others", as the frequencies of these behaviours were very low. Behaviours were recorded when they were shown for a prolonged time, which was defined as for longer than 10 seconds.

Mostly only one behaviour was shown per video, however in the case of two behaviours shown for more than 10 seconds, both behaviours were recorded.

Table 2: ethogram used for the video categorisation with BORIS

	Behavior type	Key	Code	Description
1	Point event	1	absent or not visible	not visible or absent, or the present bird cannot be identify as this individual
2	Point event	2	present	present but do no engage in any activity
3	Point event	3	maintenance	moving and bringing material or decorations, clearing unwanted objects
4	Point event	4	painting	painting the walls of the bower with chewed leaves
5	Point event	5	display alone	producing a courtship display without any visible bird
6	Point event	6	display with other(s)	producing a courtship display with other bird(s) present, in or out the avenue
7	Point event	7	receive display	attending to a courtship display while standing in the bower avenue
8	Point event	8	destructing bower	destroying the bower, in any proportion
9	Point event	9	stealing decoration	stealing decoration (generally happens after a destruction)
10	Point event	0	interact with other species	interacting with an extra-specific animal, generally an intruding animal
11	Point event	ß	conspecific agonistic interaction	attacking or being attacked by another bowerbird (generally an intruder)
12	Point event	q	crouching/cloaca dilatation	crouching to indicate copulation acceptance and/or showing cloaca dilatation
13	Point event	w	copulation	copulating (receiving or mounting)
14	Point event	e	unknown beahvior	producing an unknown or a non-categorizable behaviour, put details in notes
15	Point event	a	animal	other animal than bower bird
16	Point event	d	delete	delete video as not useable

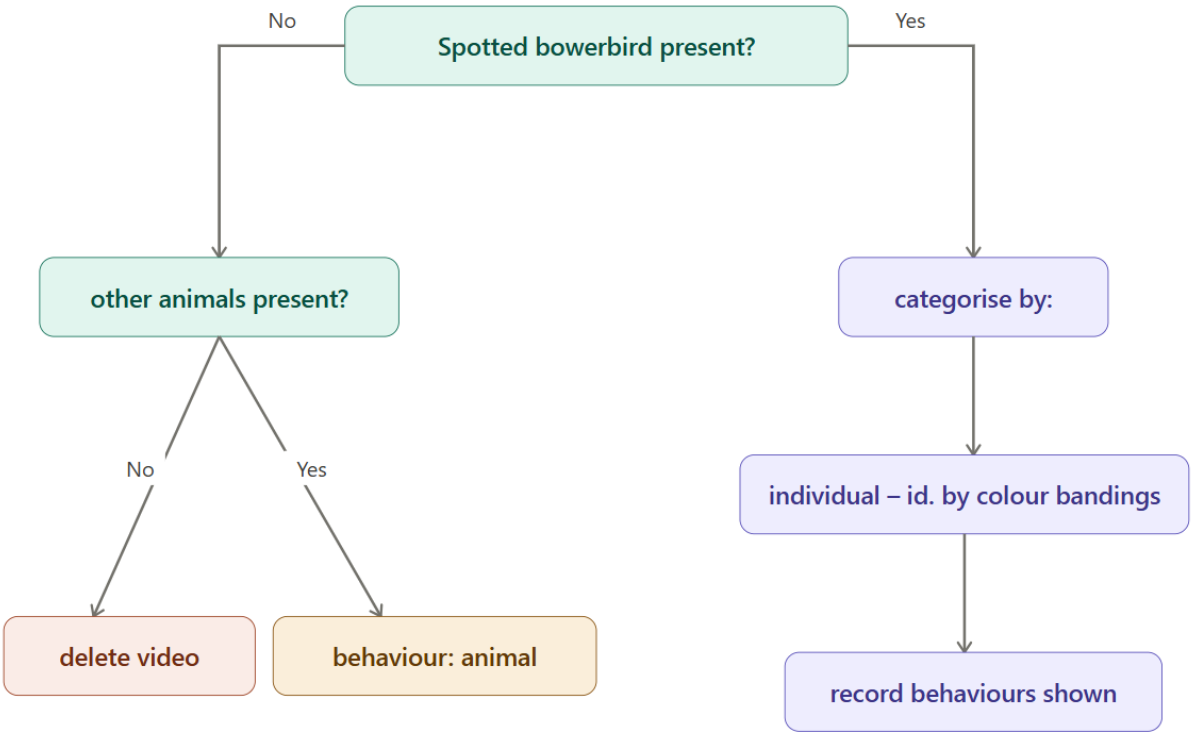

Figure 6: Scheme showing how video data was categorized

Time budget and mating success

With the help of the video categorisation, I calculated the time budgets of each bird for each behaviour. As the behaviours are usually shown for a prolonged period of time and most videos are around thirty seconds long, I approximated the duration of a behaviour to the length of the video it was shown in. If there was more than one behaviour shown in a video, the duration of a behaviour was calculated as the duration of each video divided by the number of behaviours show. Then the durations of each behaviour in all videos were summed up per individual. For each bower the proportion of time the owner spent at his bower was determined. For that, time the owner spent at his bower was divided by the total duration a camera was active at a bower.

To have a measure of how successful the bower owners were during the recording time, the number of copulations was counted for each individual. This number was corrected for the time each bower was filmed by dividing the total number of copulations by the total duration the camera was present at the bower. This resulted in copulations per second. To make the results clearer the mating success was transformed into copulations per hours. In a last step I compared the video data and mating success with a spearman correlation test (*cor.test(df_sub$prop_at_Bower_video, df_sub$cor_mating, method = "spearman")*) in R (R Core Team, 2025). As the sample size was small, I did not run a linear model.

GPS data analyses

I analysed the gathered GPS data using R (R Core Team, 2025). The Data was cleaned and filtered leaving only GPS points that were accurate. Data points that were recorded on the day of capture were discarded. To understand whether a GPS fix was recorded at the bower of a bird or away from the bower, I calculated the distance from the individuals bower for each GPS fix. This was done with the *distGeo* function from the *geosphere* package in R (Hijmans, 2026). Taking into consideration that the GPS-error can be estimated to be around 5 m (Makuya & Schradin, 2023) everything below a distance of 10 m to the bower was counted as being present at the bower and all points further away were counted as away from the bower. The chosen distance is the sum of the GPS error (5 m) and the distance that was used by Frith and Frith, 2004 for birds to be counted as at the bower (5 m). This allowed me to compute the proportion of GPS fixes that were at the bower and the number of fixes that were away from the bower. To investigate the effects

of season and year on the time spent at the bower, a GLMM analysis with the *glmer* function from the *lme4* package was done (*glmer(Location ~ season + Year + (season | Bird) + (1 | Date_AEST_factor), data = fixes_owner, family = binomial*) (Bates *et al.*, 2015). The Location (at bower / away from bower) was used as the binary response variable, with season and year defined as the fixed effects. To account for repeated measurements during a day for birds the individual bird ID and date were included as random intercepts. Furthermore, a random intercept for season by bird was included to allow individual variation in response to season. The model was checked for model fit and quality, with the *DHARMa* package (Hartig, 2026). GPS data of the mating season 2024 and mating success were compared with a spearman correlation (*cor.test(df_sub_GPS$prop_at_bower_GPS, df_sub_GPS$cor_mating, method = "spearman")*) in R (R Core Team, 2025). As the sample size was small, I did not run a linear model.

Comparison of time budgets from camera traps and GPS data

To investigate whether the GPS data and data of the camera traps co-vary I did a comparison between the calculated time-budget of the camera traps and the calculated proportion of GPS fixes at the bower. Therefore, the GPS-fixes were filtered for the time span the camera traps were active in 2024, to have a similar sampling period. A direct comparison of sampling times was not possible, as the camera traps recorded continuous data, whereas the GPS trackers provided discrete location points at specific intervals in time. Thus, the mean proportion of GPS fixes at the bower across all seasons were calculated for each individual and compared with the help of a Pearson correlation (*cor.test(video_vs_GPS$prop_at_Bower_video, video_vs_GPS$prop_at_bower_GPS, method = "pearson")*) to the time budget proportions of the camera traps. As the sample size was small, I did not run a linear model.

Vegetation survey analyses

I analysed the gathered data with R to understand what factors drive the visitation rates of the squares and therefore understand what makes a site attractive for spotted bowerbirds. To see whether a spatial GLM was needed, the model was run as a spatial GLM and as a GLM. Afterwards the AIC values were calculated with the *AIC(model)* function in R and compared (R Core Team, 2025). The AIC value is an evaluation of the model fit, the lower the value the better the model is fitted to the data (Burnham & Anderson, 2004).

Including a Matern spatial autocorrelation structure improved the model fit (ΔAIC= 192). Therefore, a spatial GLMM was fitted with the *fitme* function from the *spaMM* package (*fitme(n_visit ~ species_richness + coverage_plants + dist_bower + coverage_rest + Matern(1 |x_c + y_c), family = poisson(), data = GPS_sf_m*) (Rousset & Ferdy, 2014). The number of visits was chosen as the response variable. Although the count data of the visitation rate initially showed a strong overdispersion, meaning the variance far exceeded the expected variance (variance= 1514, mean=13.9, variance/mean ratio = 109), this overdispersion was resolved once the spatial structure of the data was taken into consideration. Therefore, a Poisson model was chosen. As fixed effects the species richness, the total coverage of focal plants, the distance of the square to the bower, and the total coverage of non-focal plants were chosen.

To account for spatial autocorrelation between square locations, a Matern correlation structure was included into the model. This models a correlation between observations as a function of geographic distance and is widely used in spatial statistics for its flexibility, particularly through a smoothness parameter (v) that allows to infer the degree of spatial correlation directly from the gathered data (Stein, 1999). Model quality was inspected visually by examining residual plots, Q-Q plots and fitted vs. observed value plots that were created with the *plot()* function in R (R Core Team, 2025). This suggested that the model not completely captured low count values and therefore underestimates the rate of near-zero observations in the data.

To see whether there is a correlation between focal plant coverage and species richness a spearman correlation with the *cor.test* function in R was done (*cor.test(GPS_sf_m$species_richness, GPS_sf_m$coverage_plants, method = "spearman"*) (R Core Team, 2025).

Results

Time budget and mating success

The time budgets computed from videos showed that on average the birds spend 3.25% +/- 1.55% of their time during the breeding season of 2024 at their bowers. However, a rather big variation concerning the time spent at the bower throughout the individuals was found, with the data ranging from 0.754% for the owner of B02 to 6.377% for the owner of B72 (Figure 7).

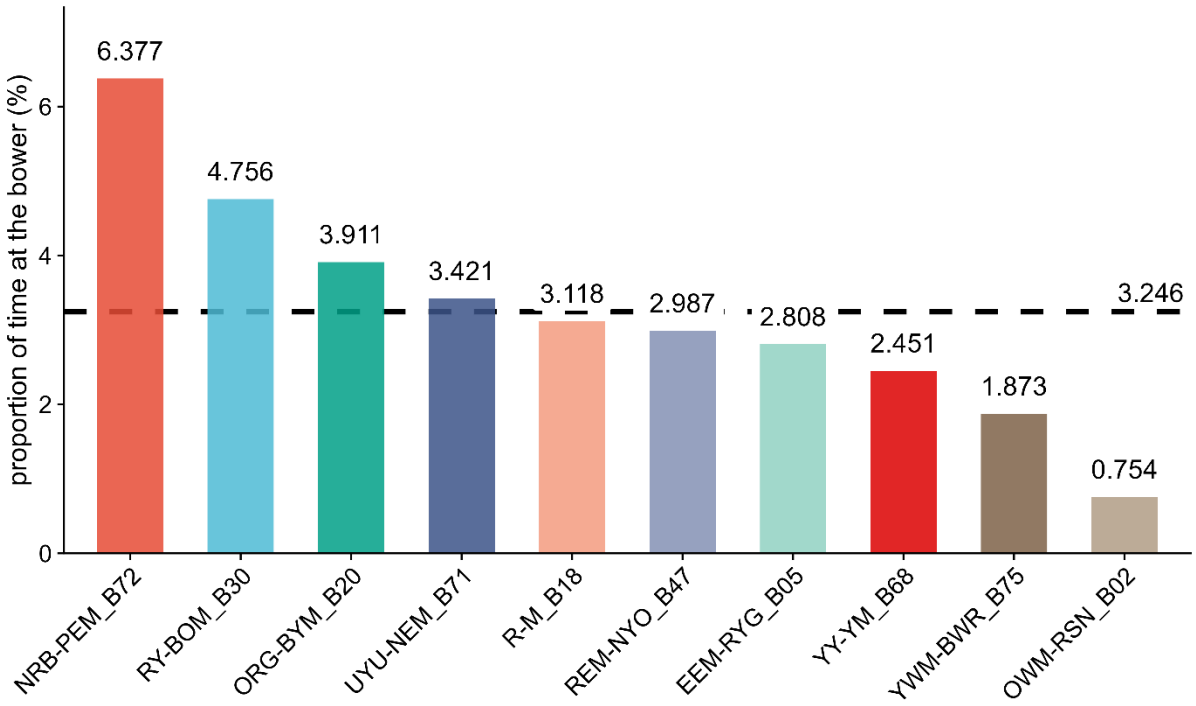

Figure 7: Histogram showing the proportion of time birds spent at their bower from the total time cameras were placed at the bower. On the y-axis the proportion in percent is shown, while on the x-axis the individuals are shown. The data points show the values of the individual birds. The dashed line marks the mean value ($\bar{x}$ = 3.246).

The video analyses with Boris gives us a more detailed insight into what's going on when the individuals are present at their bowers (Figure 8). Similarly to the result found for the time spend at the bower the owner of B72 shows the highest value in the behaviour "maintenance" with 80%. This is by far the most prominently shown behaviour throughout all individuals, whilst the owner of B02 shows the lowest value in "maintenance" with 28%. On average the birds spent 56.6 +/- 13.9% (range: 28 – 80%) of their time at the bower maintaining, 15.9 +/- 8.43% (range: 5 – 31%) being present, 9.99 +/- 8.65% (range: 0.1 – 30%) painting, 6.66 +/- 2.18% (range: 4.3 – 11%) being absent or not visible, 16.26 +/- 9.17% (range: 0.78 – 30%) displaying with others, 3.41 +/- 2.77% (range: 0.53 – 9%)

displaying alone and 1.13% +/- 1.29% (range: 0.12 – 4.39 %) doing other activities. A high variability between individuals in the categories of behaviours and proportion of the behaviours can be found. For example, the owner of B02 dedicated the most time to displaying with others (30%). On average the birds only dedicated 6.66% of their time to this behaviour. Whilst the owner of B72 predominantly maintains its bower and does little else, the owner of B75 for example has a big variation of behaviours shown, with his time more evenly spread among the behaviours.

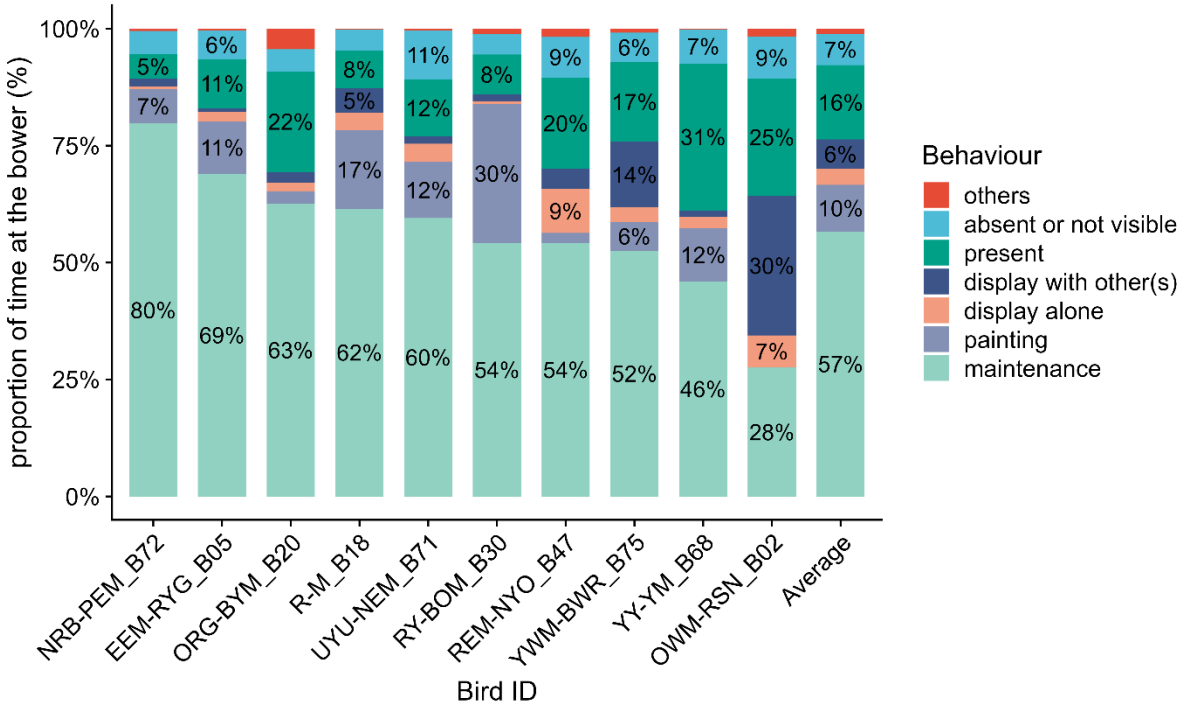

Figure 8: Bar charts showing the proportions of each behaviour that is shown at the bower. On the y-axis the percentages are displayed while at the x-axis the individuals are shown. Values below 5% are not labelled. Each bar shows the proportions for one individual. The bar on the right shows the average values across all individuals are shown. The values were rounded to full numbers for readability.

Only six of the observed ten males were able to mate during the observation period (Figure 9). The owner of bower 47 is the most successful male with 0.0039 copulations per hour. However, most individuals showed very similar mating success with 5 Individuals having between 0.003 and 0.004 copulations per hours. Only the owner of B71 showed a considerately worse mating success with 0.0011 copulations per hour.

Comparing the mating success to the proportion of time at the bower from the camera traps, with a spearman correlation revealed no significant trend (R = 0.14, p= 0.8) (Figure 10). Birds who spent more time at the bower did not necessarily have a higher mating success. The four owners who did not achieve any mating success were excluded.

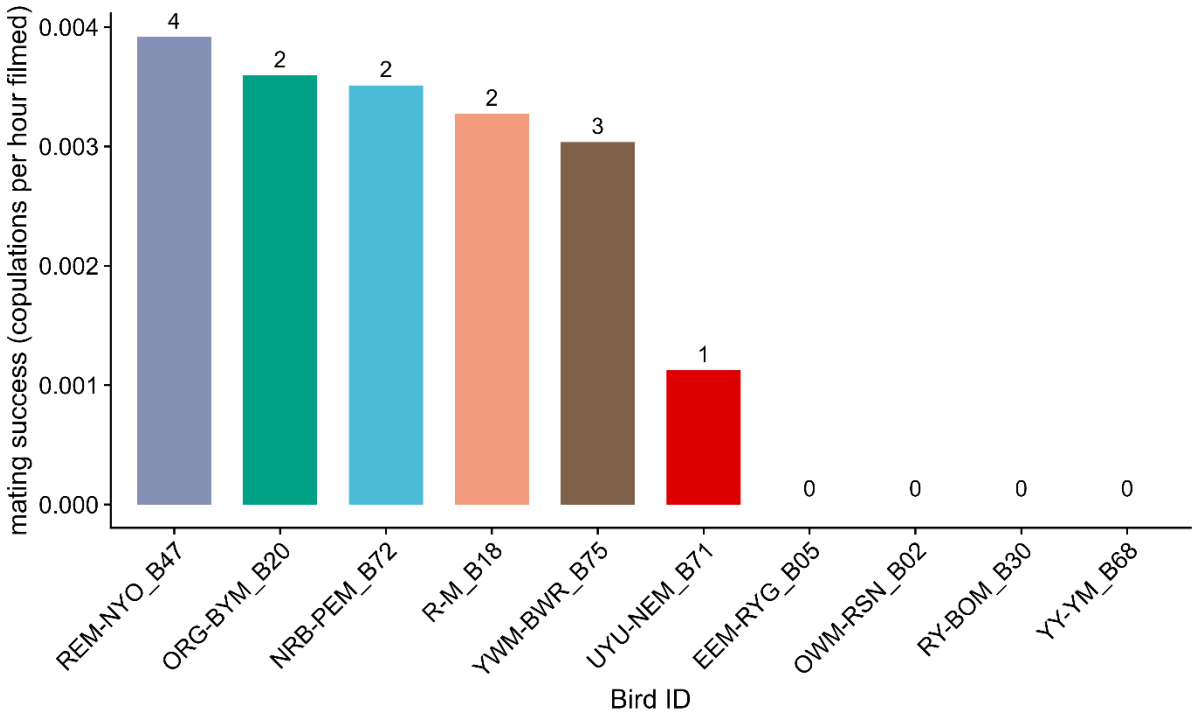

Figure 9: Bar charts indicating the number of copulations of each bower owner during the observation period. The values are corrected for the time each bower was filmed. On the y-axis the corrected values for the copulations are displayed. On the x-axis the individuals are shown. Each bar represents one individual. The labels on the bar charts display the absolutes of observed copulations per individual.

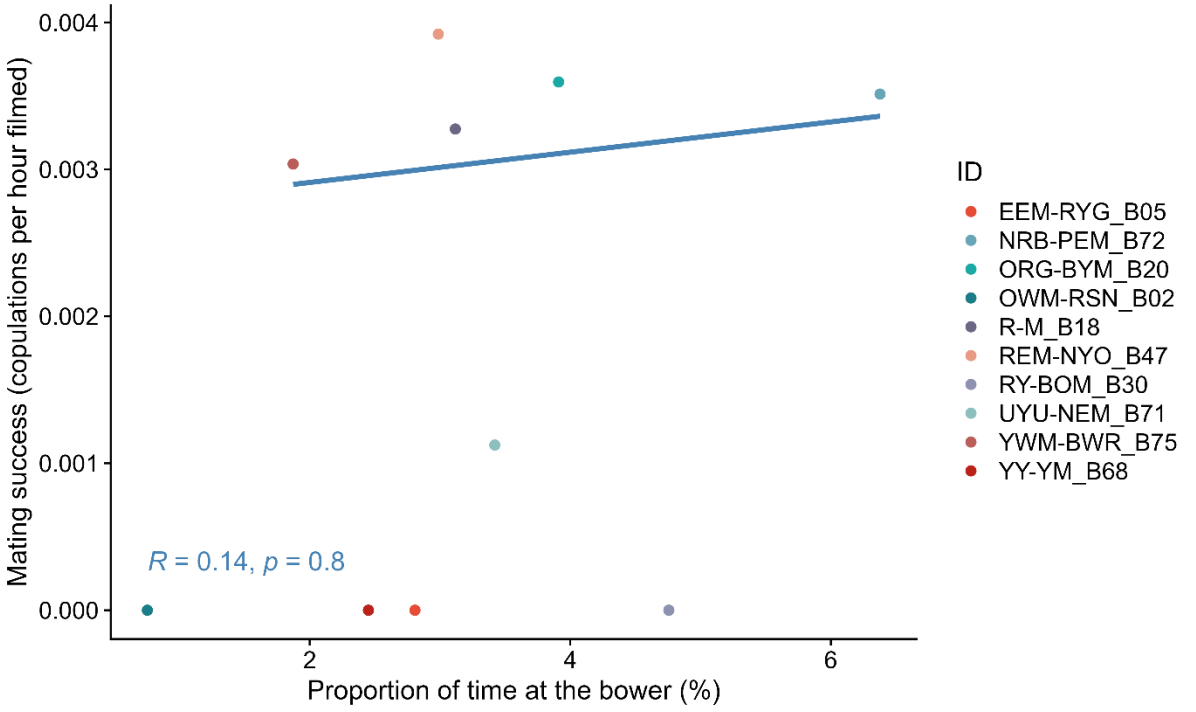

Figure 10 Comparison between the mating success and the time budget from the camera traps. On the y-axis mating success corrected for the time filmed is shown. On the x-axis the proportion of time at the bower from the camera traps in percent is shown. The data points show the individual values. In the legend the colour corresponding to each individual is shown. The blue line indicates the correlation between the two datasets. Birds with no mating success are excluded from the correlation.

GPS data analyses

When comparing individuals for the proportion of time spent in or out of the bower from the GPS fixes, individuals were significantly less often present at the bower during the non-breeding season (GLM β = -2.51, SE=0.71, z=-3.53, $p < 0.001$) in comparison to the breeding season. Furthermore it showed that in the Year 2021 the bower attendance was lower in general in comparison to the reference year 2018 (GLM β = -2.81, SE = 0.60, z = -4.68, $p < 0.001$), whilst the year 2025 was significantly higher in bower attendance (GLM β = 0.92, SE = 0.47, z = 1.96, p = 0.0498). Apart from that no other years differed significantly from the year 2018.

The model was able to explain 21.7% of variance in attendance of the bower through fixed effects alone (marginal R^2 = 0.217). However, when including random effects, the model was able to explain 62.1% (conditional R^2 = 0.621; Nakagawa & Schielzeth, 2013). The large difference can likely be explained due to variation between individuals and variation in dates the fixes were recorded.

Looking at the proportion of GPS fixes at the bower a large variation between individuals and seasons can be found (Figure 11). The data ranges from 0 to 27.3% in the breeding season. The variation is smaller in the non-breeding season (0 - 13.6%) but still considerable. For the individual "YGO-M", which showed zero percent bower presence in the courtships season I only have a small number of GPS-fixes during the month November of 2019. On average 12.8 +/- 7.77% of the GPS fixes during the "breeding season" were at the bower whilst it was only 5.6 +/- 5.54% during the "non-breeding season".

Comparing the mating success with the proportion of GPS fixes at the bower of the mating season 2024 with a spearman correlation revealed no significant trend (R= -0.086, p= 0.92) (Figure 12). Birds who had more proportion of fixes at the bower did not show different mating successes than bird with less GPS fixes at the bower. The four owners who did not achieve any mating success were excluded.

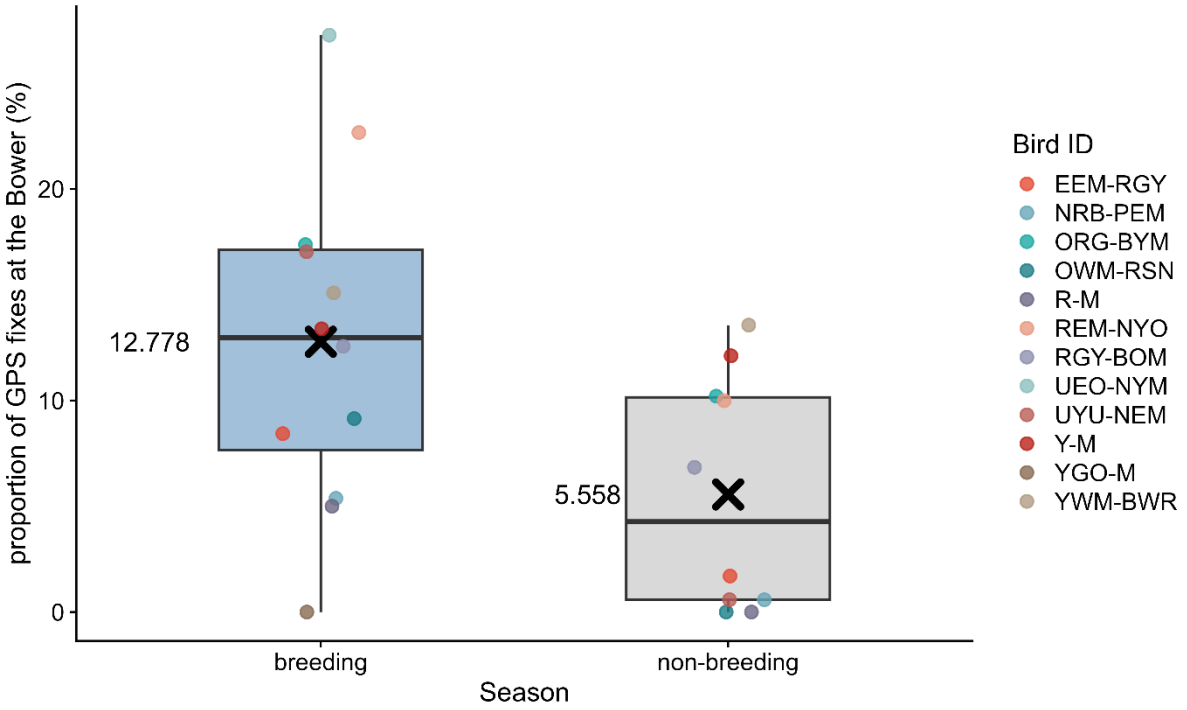

Figure 11: Boxplots showing a comparison between seasons for the proportion of GPS fixes at the bower. One boxplot shows the values for the breeding season whilst the second shows the values for the non-breeding season. On the y-axis the percentages for the proportion at the bower are shown, on the x-axis the two seasons are shown. The points show the individual values of the birds marked in different colours. In the legend the colour corresponding to each individual is shown. The black x indicates the mean values for both seasons. $\bar{x}$ = 12.778 for the courtship and $\bar{x}$ = 5.558 for the non-breeding season.

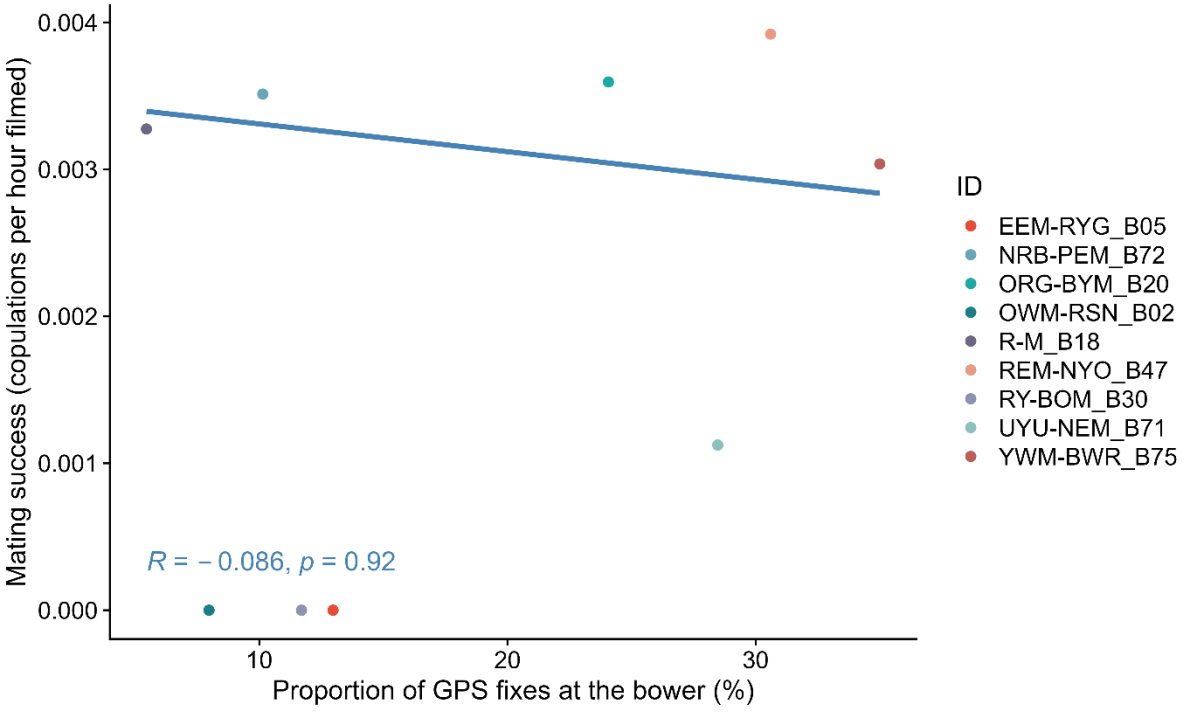

Figure 12 Comparison between the mating success and the proportion of GPS fixes at the bower. On the y-axis mating success corrected for the time filmed is shown. On the x-axis the proportion of GPS fixes at the bower from the GPS data in percent is shown. The data points show the individual values. In the legend the colour corresponding to each individual is shown. The blue line indicates the correlation between the two datasets. The correlation takes the data points with no mating success not into consideration.

Comparison time budget camera traps and time budget GPS

Comparing the time budgets gathered from the video data with the proportion of GPS fixes at the bower with the help of a Pearson correlation, revealed no significant relationship (R= -0.19, p=0.63) (Figure 13). Birds that had a higher proportion of being at the bower did not show a higher proportion of being at the bower in the GPS data.

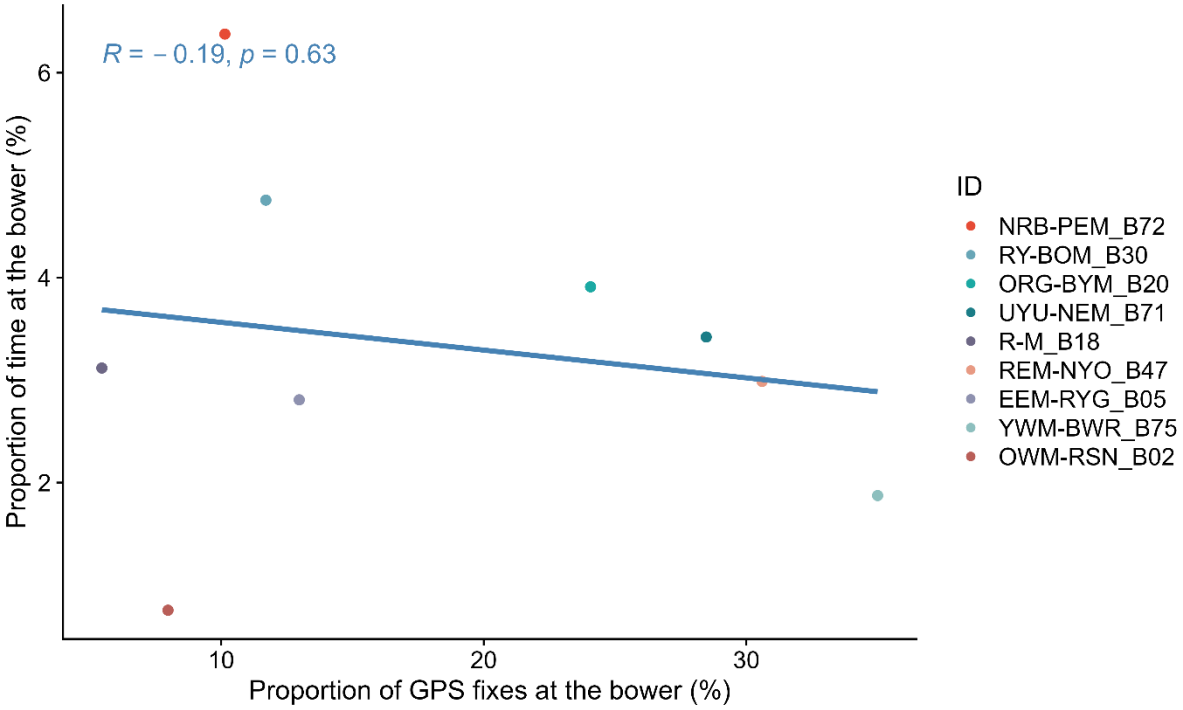

Figure 13 Comparison between the time budget from the camera traps and the proportion of GPS fixes at the bower from the GPS. On the y-axis the proportion of time at the bower from the camera traps in percent is shown. On the x-axis the proportion of GPS fixes at the Bower in percent is shown. The points show the individual values. In the legend the colour corresponding to each individual is shown. The blue line indicates the correlation between the two variables.

Vegetation survey analyses

The vegetation analyses showed that squares with a higher focal plant coverage had significantly higher visitation rates than squares with a lower focal plant coverage (spatial GLMM, β= 0.0065, SE=0.003, X^2=5.17, p=0.023) (Figure 14c). The distance to the bower is a significant negative predictor (β=- 0.0004, SE=0.0002, X^2=6.84, p=0.0089) (Figure 14b). This indicates that the further away a square is from the bower the lower is the visitation rate. The focal plant species richness (β=- 0.0505, SE= 0.0574, X^2=0.77, p=0.38) and non-focal plants coverage (β=0.0013, SE= 0.0039, X^2=0.12, p=0.732) did not have any effect on the visitation rate. A significant spatial autocorrelation in visit frequency was

found (λ= 1.512, v=0.443, ρ=0.022). The biodiversity in a square and the focal plant coverage of said square are positively corelated with each other (R= 0.46, p < 0.001) (Figure 15).

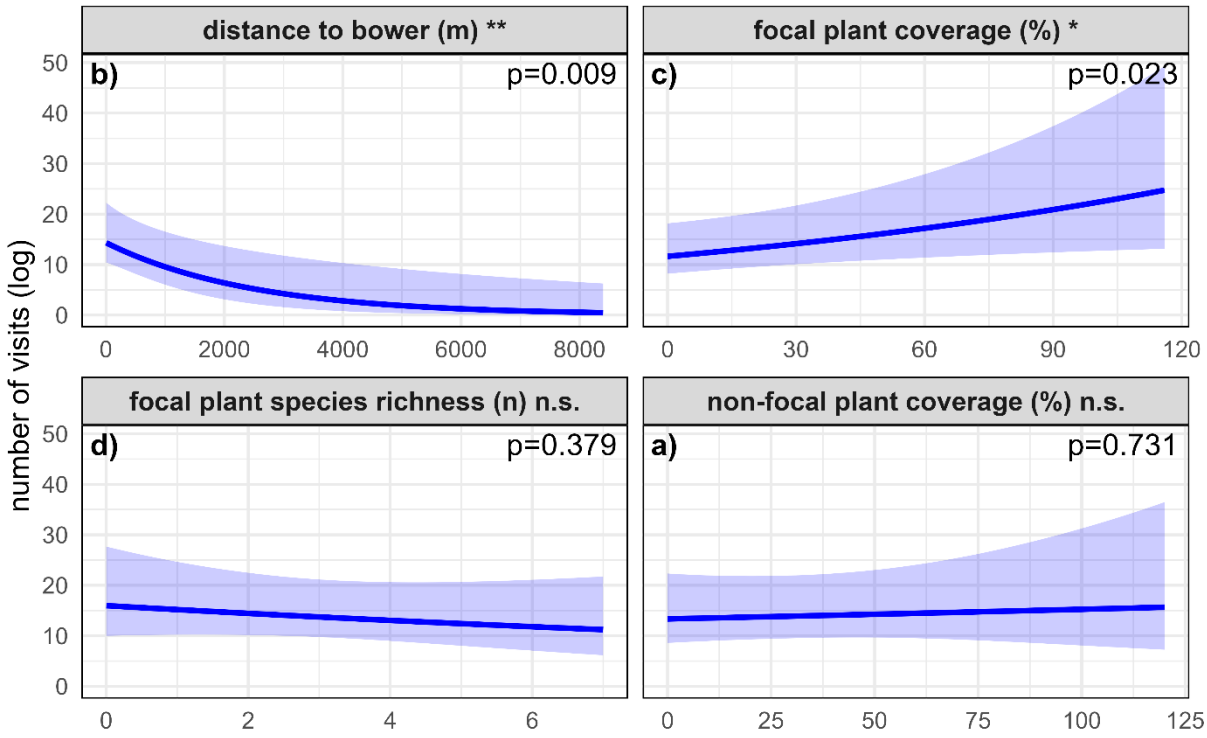

Figure 14 Effects of the predictors on the squares' visitation rate. On the y-axis the log transformed number of visits is shown. The x-axis is specified in each plot title. a) Influence of non-focal plant coverage is shown. The effect was not significant (p= 0.731). The x-axis shows the coverage of plants in %. b) Effect of the distance of the square to the bower is shown. The effects were significant (p= 0.0087). The x-axis shows the distance in meters. c) Effect of the focal plant coverage of plants of interest is shown. A significant effect can be seen (p=0.023). The x-axis shows the focal plant coverage in percent. d) species richness for plant species of interest is shown. There is no significant effect (p= 0.379). The x-axis shows the number of species.

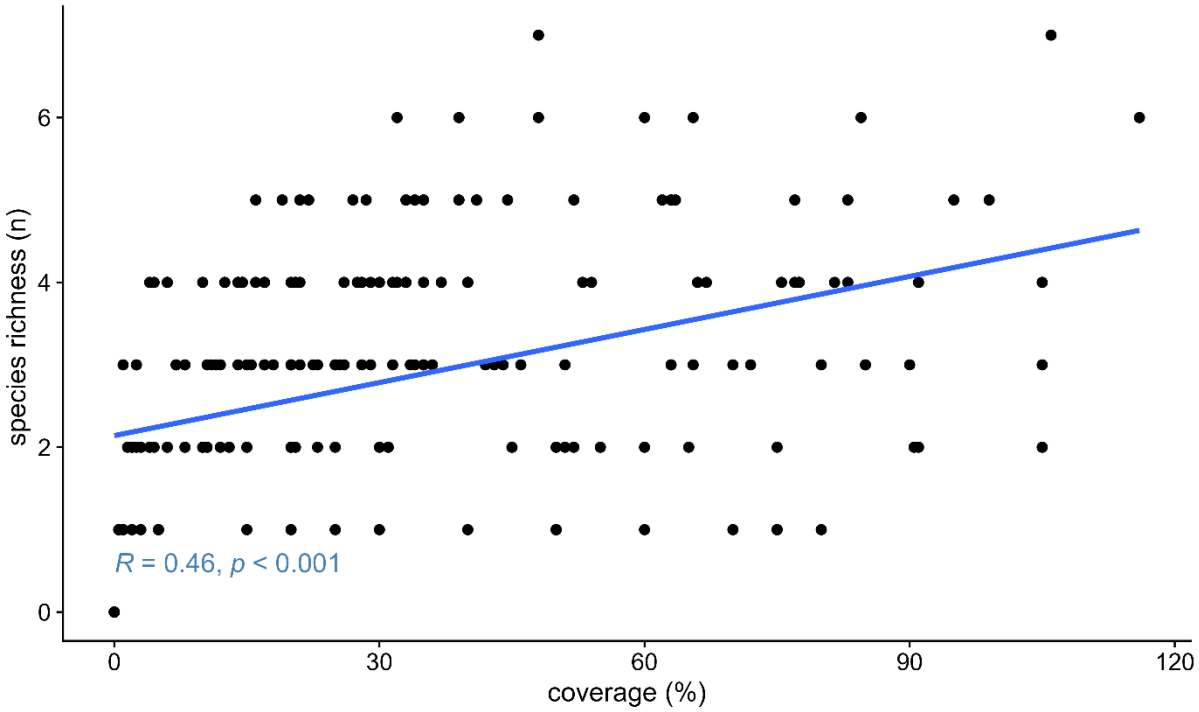

Figure 15 shows the species richness of the square in comparison to the focal plant coverage of species of interest of the squares. On the y-axis number of species is shown. On the x-axis the focal plant coverage in percent is shown.

The following results are descriptions of the vegetation analyses giving a better understanding of the vegetation in Taunton National Park (Scientific) (Figure 16 to Figure 20). The average square, among squares that have at least one visitation, is visited 13.9 +/- 38.9 times (range: 1 – 351) and shows 32.2 +/- 28.3% (range: 0 – 116%) focal plant coverage whilst it has a species richness of n=2.83 +/- 1.52 (range: 0 – 7). On average a visited square is 360.56 +/- 861,89 m (range: 4.6 – 8399.44 m) away from the bower and has a non-focal plant coverage of 24.14 +/- 22.89% (range: 0 – 120%). The currant bush *(Carissa ovata*), present in 123 squares, and Brigalow *(Acacia harpophylla*), present in 116 squares, were by far the most encountered species during the vegetation analyses (Figure 16). There were also a few species that were hardly present in any squares such as the Desert lime *(Citrus glauca)* which was only found in 3 squares.

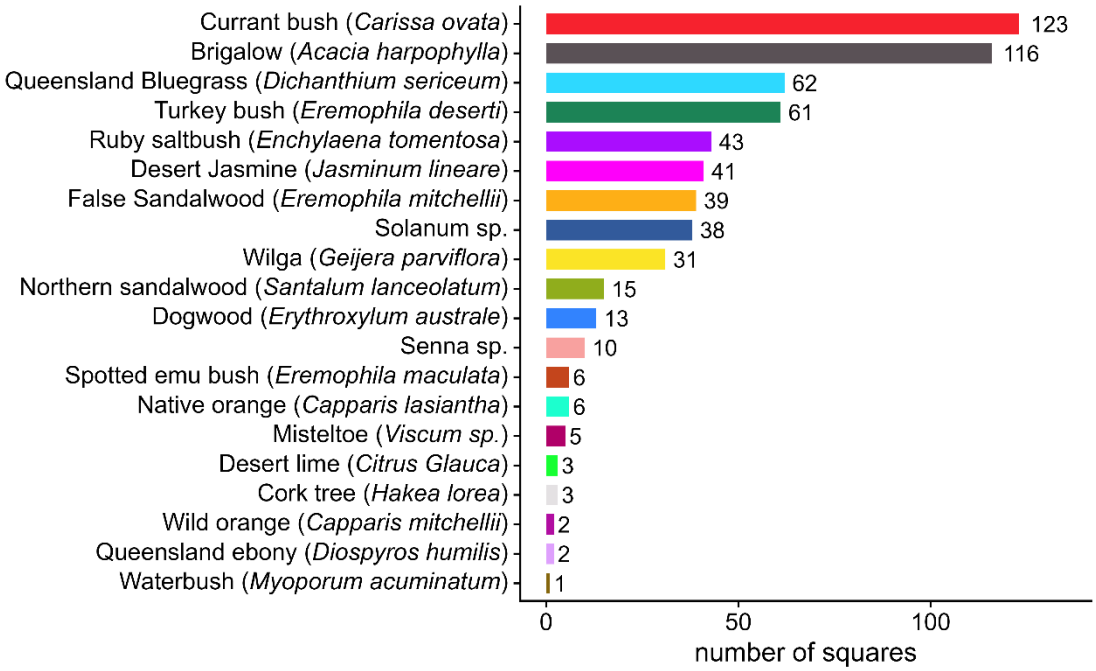

Figure 16 Histograms showing the number of squares in which a focal plant species is present. On the y-axis the species names are shown. On the x-axis the number of squares is shown.

Looking at the variation in coverage per species no general pattern can be found (Figure 17) although a considerable variance in coverage exists. However, some species like *Solanum* sp. or the ruby salt bush (*Enchylaena tomentosa*) show only very little variance in coverage. Even though these species were present in about 15 to 20 percent of all squares (Figure 16). When looking at the total focal plant coverage of the squares a rather big variation can be observed throughout nearly all species (Figure 18). Exceptions are plants like the Waterbush (*Myoporum acuminatum*), which are found in only very few squares (Figure 16), therefore the variation is also little. Also, in only very few squares that were analysed was just one species present (Figure 19). Mostly at least 2 species of interest were present, and no plant species shows a trend to be present only in squares with very little diversity. Additionally, to the coverage of the plant species of interest, also the coverage of species that were not of interest was recorded. Comparing Figure 20 to Figure 18, it seems that plants of interest were more common and showed higher coverage than plants that were not of interest in the sampled squares. For further insights three more figures describing the vegetation and relationships between the predictors can be found in the supplementary materials (Figure S 1 – Figure S 3).

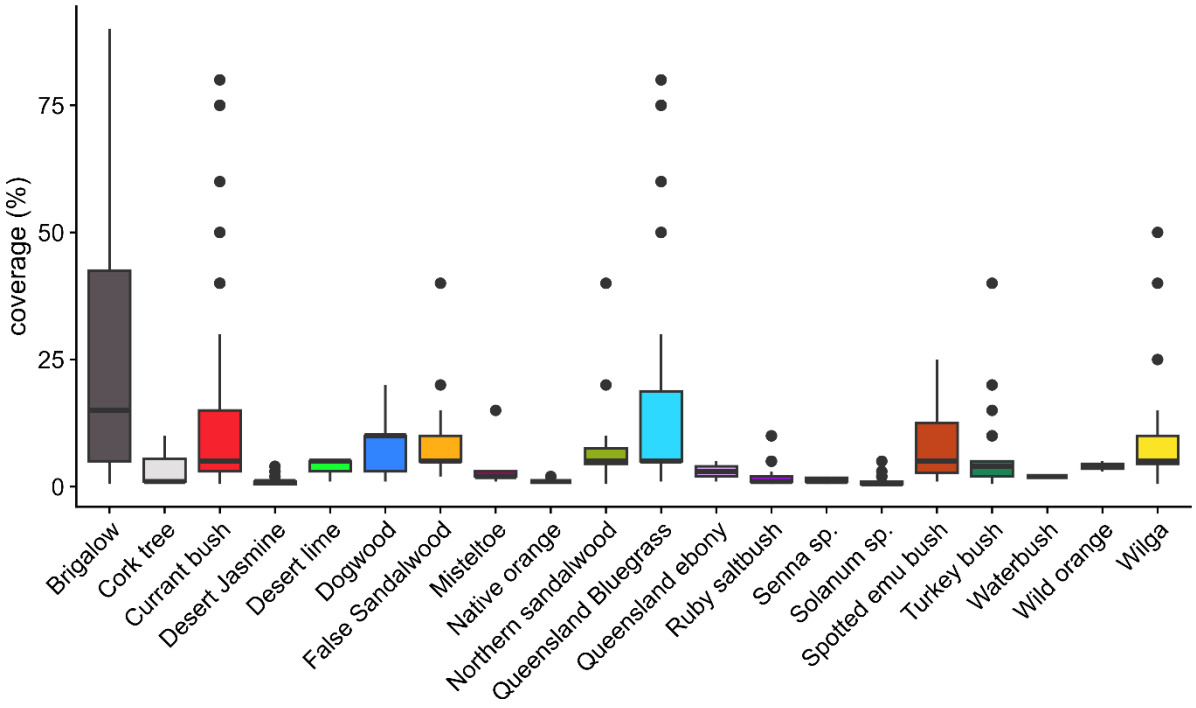

Figure 17 Boxplots showing the coverage of each focal plant species for each square where the species is present. On the y-axis the coverage in percent is shown. On the x-axis the common species names are shown.

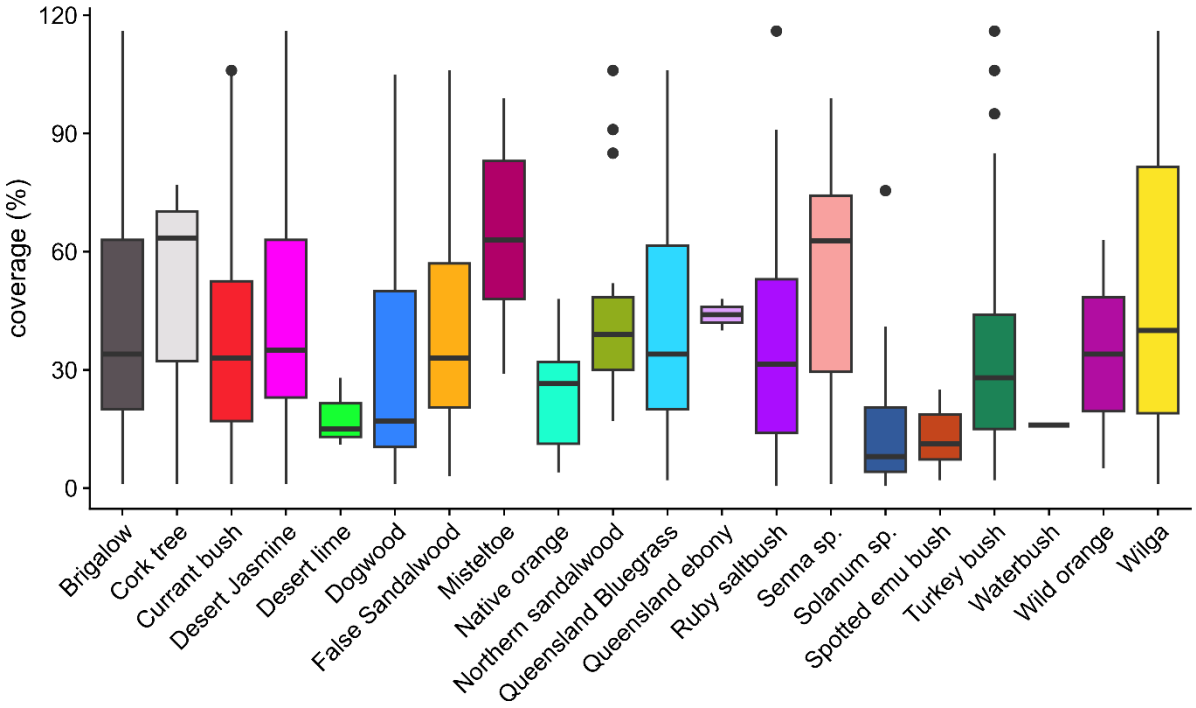

Figure 18 Boxplots showing total focal plant coverage for all focal plants combined of squares where species is present. On the y-axis the focal plant coverage in percent is shown. On the x-axis the common species name is shown.

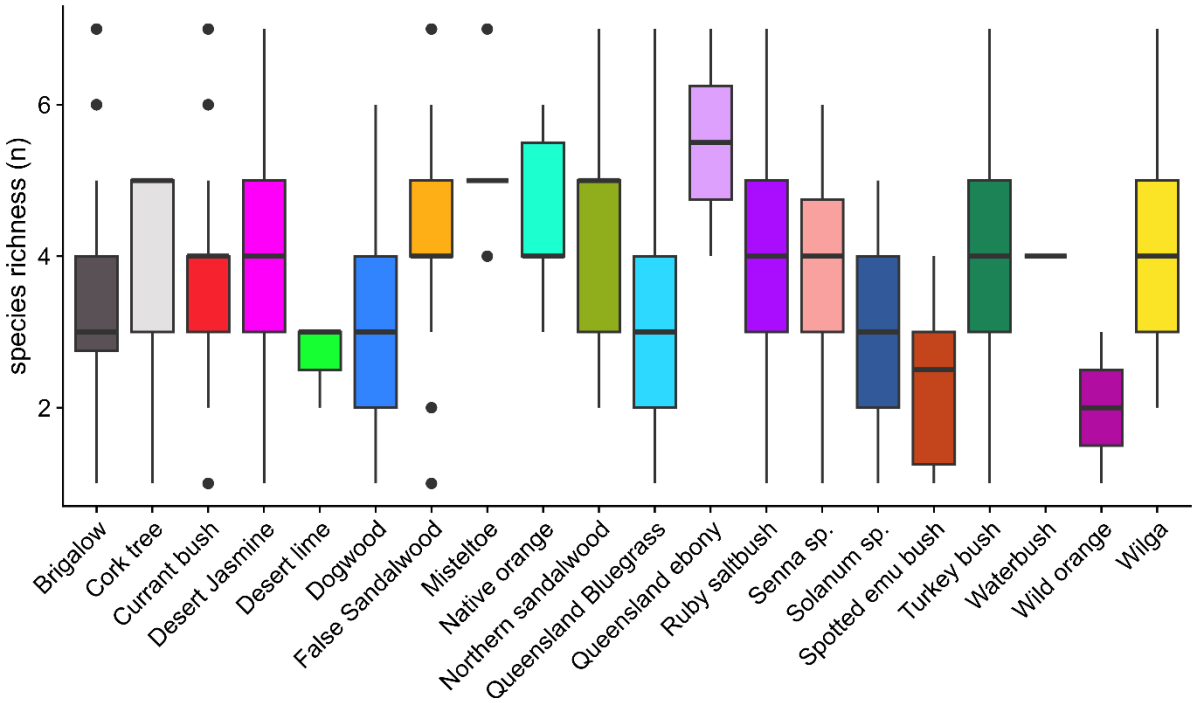

Figure 19 Boxplots showing the plant species richness of squares where a specific focal plant species is present. On the y-axis the number of species is shown. On the x-axis the species names are shown. Each boxplot shows the values of one species.

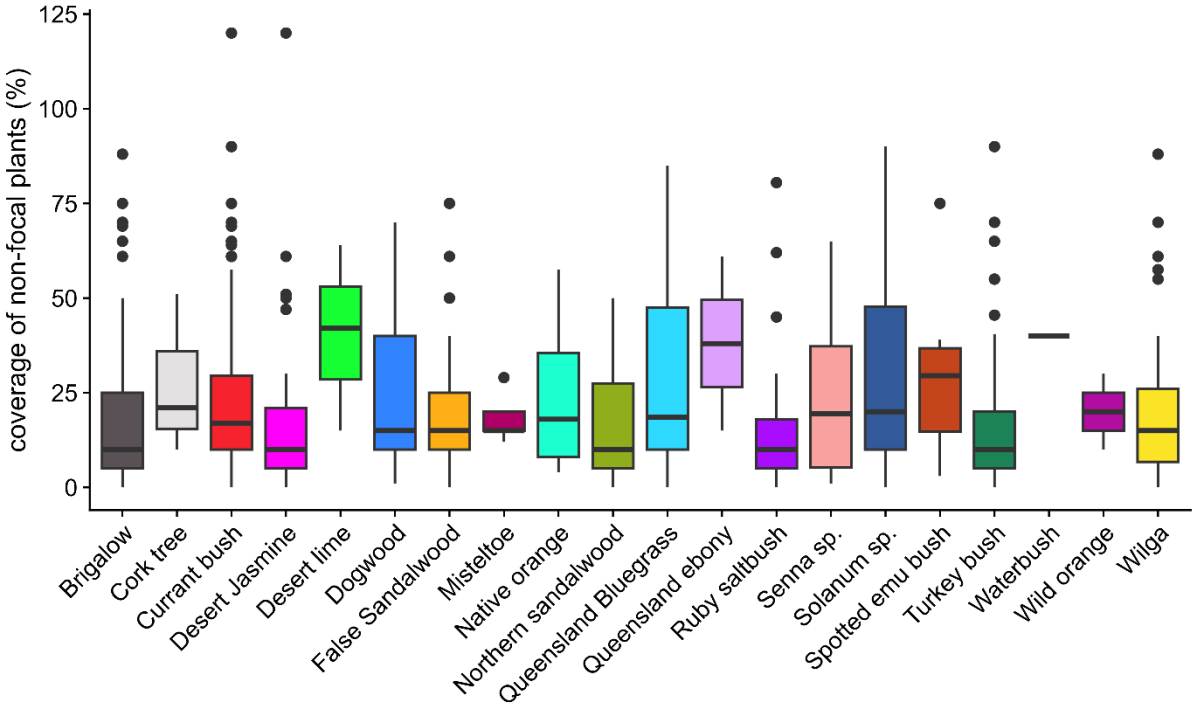

Figure 20: Boxplots showing the variation in coverage of non-focal plants, in squares where a focal plant species is present. On the y-axis the non-focal plant coverage in percent is shown. On the x-axis the species name is shown. Each boxplot shows the values for each species.

Discussion

In this thesis, I investigated costs of spotted bowerbird's courtship through time budget differences between breeding and non-breeding season, using camera traps and GPS tracking devices. Combining GPS data with video data of the breeding season was a novel approach that revealed significant differences in behaviour between the two seasons, with the birds spending significantly less time at the bower during the non-breeding season. Furthermore, the vegetation analyses revealed that birds more often visited sites in the environment that are closer to their bower and offer a higher coverage of plants that are used for foraging.

Male spotted bowerbirds spent on average around 3.25% of their time during the breeding season at their bower. In comparison to the existing literature, the observed time budgets from the video analysis seem to be low. For example, Frith & Frith (2004) state that male spotted bowerbirds spend around 36% of their time during daylight hours at the ground in their bower engaged in bower-related activities. However, it should be noted that the methods differed significantly. In the present study, camera traps were set up at a standardized distance to record bower activity and remained in place the entire season. Frith & Frith (2004) conducted in person observations at the bowers for 48 hours. Furthermore, neither the exact time of the year of the observations nor the quality of the season are reported. It has been found that seasons with more rainfall are characterised by higher levels of precipitation and higher bower activities (Isden et al., 2025). It is therefore possible that the time of observation coincided with a season of higher quality. However, camera traps are subject to limitations as well. The restricted field of view can lead to birds being present at the bower but out of camera frame. Therefore, the measured time budget may be lower than the actual time budget. This is supported by the fact, that I found considerably higher proportions of GPS fixes at the bower with the GPS analysis. On average 12.78% of the GPS fixes were at the bower during the breeding season. For the GPS data a radius of 5 m +/- 5 m GPS error around the bower was assumed. However, vertical position was not considered, such that any fix falling inside the radius was assumed to be present at the bower. Comparing the two different methods to gather presence at the bowers revealed no significant correlation. An explanation for the differences between the methods may be caused by inter-individual variation. It could be that some

individuals may stay in the proximity of the bower —outside of the camera range— to defend it from rivals, whilst other individuals allocate their time more to bower maintenance and other courtship behaviours. It has been reported that bower owners regularly sit in the canopy above the bowers calling for females (Frith & Frith, 2004). When comparing the results to time budgets that were also gathered with camera traps the results are more similar (Isden et al., 2025). Moreover, Isden et al., 2025 calculated time budgets for three continuous seasons, with the precipitation being measured as a predictor for the quality of the season in the context of bower attendance. The lowest bower presence was found in the driest year (~ 2%), whilst moister years showed around 6% (Isden et al., 2025). In my study I found on average a 3.25% presence at the bower, which is more comparable to the driest year. However, as there is no recorded weather data for the season of 2024, the season quality in terms of precipitation cannot be assessed.

Additionally, I observed a considerable inter-individual variation in the presences at the bower. Such individual variation could be related to differences in male quality in terms of reproductive success. However, I found no correlation between the mating success and the time investment into the bower in either method. This could indicate that bower presence alone is an insufficient predictor for mating success as it may also depend on the specific behaviours that are shown whilst being present at the bower. As only 6 out of 10 individuals achieved at least one copulation, the sample size could be insufficient to conclude a meaningful result. Further, the inter-individual variation could be caused by differences in the age of the males. It has been found in great bowerbirds (*Chlamydera nuchalis*) that individuals who were owners for a longer time exhibited fewer solitary courtship displays (Doerr, 2010), potentially resulting in a lower total time investment. Differences in courtship display rates and durations have also been found in spotted bowerbirds of different age related breeding stages, namely subordinate males and bower owners (Spezie & Fusani, 2022).

When the birds are away from the bower, a big portion of the time budgets is likely dedicated to foraging. It is not fully known what makes a foraging site attractive for spotted bowerbirds. In this study I found that birds visit sites with a high focal plant coverage significantly more often. By contrast, the focal plant species richness does not influence the visitation rate. A greater coverage may increase the amount of food that is available, lead-

ing to birds spending more time there to feed on the offered resources. Furthermore, because a higher coverage of focal plants is easier to find, it may lead to a higher detectability of a site from above. Consequently, sites with a greater focal plant coverage are more visited than sites with only little coverage regardless of focal plant species richness. Focal plant species richness alone is an insufficient predictor, as some plants, like Solanum sp., are very small. Focal plant species richness per square was on average 2.83 with little variation throughout all squares. However, a significant positive correlation between the focal plant species richness and the focal plant coverage was found. As predicted, the coverage of non-focal plants did not influence the visitation rate of squares. On average focal plant coverage (32.2%) was considerably higher than non-focal plant coverage (22.89%). This supports the list of species that was used for the vegetation survey.

Another factor that significantly influenced the visitation rate was the distance of the squares to the bower. It is energetically efficient to minimise travel distances, and when resources are equivalent but differ in distance, it is inefficient to visit the one further away. Isden *et al.*, (2025) observed that birds with more foraging sites close to their bower collected higher numbers of decorations. Although decoration abundances were not assessed in our squares due to their minimal frequencies, the reduced distance of foraging sites to the bower seems to be important in saving time for other activities. This could be tested in the future by looking at the distances of foraging sites for each individual and comparing those to the bower attendances of the individuals. The vegetation survey of the present study revealed what the birds do when they are away from the bower and how this influences their time budgets. Birds who have their bowers closer to more suitable foraging sites may be able to invest more time into the bower during the courtship season.

The GPS analyses revealed that bower owners are also present at the bower during the non-breeding seasons. Earlier literature suggested that male spotted bowerbirds completely abandon their bower during the non-breeding season and even flock together with other individuals (Frith & Frith, 2004). However, a recent study indicated that bowers owners are present at their bower during the non-breeding season (Spezie et al., 2025). These findings, partly based on the same dataset, aligns with the results of my study, although Spezie et al. (2025) used a spatial recursion analysis without calculating proportion of fixes at the bowers. Furthermore, the present study shows that the individuals spent sig-

nificantly less time at the bowers during the non-breeding season than during the breeding season. This difference in time allocations indicates that the males time budget changes between the two seasons. The higher time investment and presence at the bower in the breeding season suggests that males invest more time into courtship behaviours and the bower than in the non-breeding season, leaving less time for other behaviours crucial to survival such as foraging. The lower proportions of presence at the bower in the non-breeding season may be caused by the absence of courtship displays or bower maintenance outside the breeding season. The video analyses revealed that the birds predominantly show courtship behaviours when they are directly at the bower in the breeding season, indicating that courtship behaviours mostly occur on the ground and not in the canopy. This is supported by the fact, that no correlation between the proportions of being "at the bower" from the video and GPS data was found. This could mean that birds, which are "at the bower" by the GPS data are not necessarily there because of courtship behaviours. This suggests that the birds may not maintain their bowers during the non-breeding season but may stay up in the canopy and visit the site predominantly to defend their territory, given that the bower is an integral part of the male's territory. Furthermore, it could be that the bower sites are in the centre of the home range of the birds and therefore the birds pass by more often. Therefore, the birds would visit the bower the same amount of time all year round if courtship behaviours would not exist. The results of this study suggest that the extra investment into the bower in the breeding season is because of courtship behaviours. This imposes extra costs on the male's time budget as they have to reallocate time, which they usually use for foraging, into courtship behaviours during the breeding season. Therefore, a trade-off between foraging and courtship behaviours can be found.

The results of this study support the use of GPS tracking to quantify presence at the bower in male spotted bowerbirds and understand activity patterns beyond the bower. As predicted, the observed courtship behaviours are time-intensive and significantly influence the time budget in the breeding season. This trade-off between courtship behaviours and foraging is common in the animal kingdom and has been documented in many bird species, especially in lekking birds such as the sharp-tailed grouse (*Tympanuchus phasianellus*), which invest less time into foraging and more time into courtship behaviours with increasing numbers of present females (Cowles & Gibson, 2015). A similar pattern

was found in Ruffs (*Philomachus pugnax*), where some males forego foraging in the breeding season to be able to invest more time into courtship displays (Lank & Smith, 1987 but see Bachman & Widemo, 1999). It has been hypothesized in songbirds that time investment in courtship behaviours such as vocalizations can reduce the time availability for foraging and therefore impose costs (Nowicki & Searcy, 2005; Thomas *et al.*, 2003). Similar findings are also reported in ungulates, where the males diminish their foraging efforts and increase their time investment in mating efforts during the breeding season (Stone *et al.*, 2017) and in male carpenter frogs (*Lithobates virgatipes*), where a trade-off between mating behaviours and growth during the breeding season was found (Given, 1988). However, Isden *et al.*, 2025 found that the time investment into courtship behaviours is limited by the resource availability, indicating that higher time investments occur in seasons with sufficient resources. By contrast, drier seasons lead to lower time investments into the bower. A similar correlation was found in white-bearded manakins (*Manacus manacus*). Males with a higher resource availability in the close environment showed higher courtship display rates and a higher mating success (Anderson *et al.*, 2024b). This suggests that foraging resources can limit the time investment into courtship behaviours. Furthermore, it has been found in satin bowerbirds (*Ptilonorhynchus violaceus*) that the survival rate does not change between the breeding and non-breeding season (Borgia, 1993). This suggests that the total possible costs of courtship behaviours in bowerbirds may be influenced by the resource availability and is not sufficient to affect death rate.

To understand those trade-offs in more detail future research should examine such differences at a finer scale. The present study only compared the seasons. Partitioning the GPS data by months or even weeks would allow us to understand the transition between seasons in more detail to see whether the increase in bower attendance from the end of the non-breeding season into the breeding season is slow or fast. It would further reveal whether the bower attendance changes throughout the breeding season. Furthermore, to determine what the birds are doing at the bower in the non-breeding season, camera traps could be installed at the bowers during this time. This would reveal why the individuals are present at their bowers during the non-breeding season, allowing us to make the distinction between the bird being in the centre of its home range or in the surrounding of the bower. The vegetation survey could be split by season and by bird to understand the

trade-offs in the breeding season more thoroughly. This would allow the comparison of time investment into foraging across breeding and non-breeding seasons and across individuals. Therefore, the time investment when the birds are away from the bower would be more quantifiable. Additionally, the vegetation survey could be refined, incorporating blooming and fruiting periods of the plants and adjusting the GPS data for those periods to determine whether temporal alignment with resource availability influences the visitation patterns. This would include partitioning the data in smaller time portions such as months or weeks to analyse and compare those time portions across each other. Understanding the visitation patterns to foraging sites in more detail would also help revealing in more detail what the birds do when they are away from the bower. Therefore, this would help to determine the costs of trade-off between foraging and courtship behaviours in more detail. Finally, to better understand the relationship between courtship time investment and mating success, a more comprehensive analysis with as many individuals as possible and across years should be carried out. Such a study would contribute to a more complete understanding of the role of time investment within the broader context of courtship behaviours and mating success in animals.

Conclusion

Combining all the gathered data I acquired a basic understanding of the behaviour of the male spotted bowerbirds throughout the year. The camera traps showed us that the birds dedicated most of their time at the bower to various courtship behaviours. Combining that knowledge with the GPS data we can see that the courtship behaviours are indeed costly and occur predominantly in the breeding season as the birds are significantly less often at the bower in the non-breeding season. This shows that there is a significant difference in the time budgets between the breeding and non-breeding season. Birds must invest more time into courtships behaviours during the breeding season and therefore can invest less time into other essential activities such as foraging. Furthermore, with the vegetation analysis I also gathered a basic understanding what the birds are doing when they are not present at the bower and what sites they are attracted to.

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Deutsche Zusammenfassung

Sexuelle Selektion wird seit langer Zeit erforscht, jedoch gibt es nach wie vor unbeantwortet Fragen, da sexuelle Selektion in unzähligen Formen auftreten kann. Eine dieser nicht vollständig geklärten Fragen ist, ob sexuelle Selektion mit Kosten für die betroffenen Individuen verbunden ist und wenn ja, in welcher Form. In dieser Studie habe ich Fleckenlaubenvögel (*Chlamydera maculata*) verwendet, um die Kosten des Paarungsverhaltens in Bezug auf die Zeitverteilung auf die unterschiedlichen Aktivitäten zwischen der Paarungszeit und der Nebensaison zu vergleichen. Außerdem habe ich eine Vegetationsanalyse durchgeführt, um zu verstehen, welche Nahrungsplätze Fleckenlaubenvögel bevorzugen. Fleckenlaubenvögel bauen Strukturen, die als Laube bezeichnet werden und vom Männchen als Bühne für ihr Balzverhalten gegenüber Weibchen genutzt werden. Da der Bau dieser Struktur zeitaufwändig ist, habe ich untersucht, ob signifikante Unterschiede in der Zeitverteilung der Männchen zwischen der Paarungszeit und der Nebensaison vorzufinden sind. Sollten signifikante Unterschiede vorliegen, kann man einen trade off zwischen Fortpflanzungsverhalten und Überleben erkennen. Die für das Paarungsverhalten verwendete Zeit kann zum Beispiel nicht für die Nahrungssuche genutzt werden. Ich habe Wildkameras und GPS-Tracking genutzt, um Zeitbudgets zu erfassen und habe diese saisonübergreifend verglichen. Ein Vergleich der beiden Methode zeigte keine Korrelation. Außerdem fand ich keinen Zusammenhang zwischen Zeitinvestment und Paarungserfolg. Wenn die Vögel auf Nahrungssuche sind bevorzugen sie Orte, die nah an ihrer Laube sind und eine hohe Pflanzenbedeckung aus Nahrungspflanzen aufweisen. Die GPS daten zeigten, dass Männchen in der Nebensaison signifikant weniger Zeit in ihrer Laube verbringen als während der Paarungszeit. Dies deutet auf Unterschiede im Zeitbudget zwischen Paarungszeit und Nebensaison hin. Die Ergebnisse legen nahe, dass Fortpflanzungsverhalten tatsächlich mit Kosten für das Individuum verbunden sind, zumindest aus der Perspektive des Zeitbudgets.

Supplementary

Video categorisation protocol

General information:

The video categorisation process aims to label each video with which individuals are present and what are the general behaviours performed by these individuals in the videos. The goal is to be then able to quickly extract a subset of videos for further detailed analyses.

The videos are stored on two hard drives and one cloud copy. A 4th separate copy is given to the person in charge of the categorisation process. On the hard drives, the videos are stored in a folder named "video_bower_start-date_end-date_original-hard-drive_backup-hard-drive". In this folder there are folders with bower names.

Categorisation protocol:

The videos are analysed in the program BORIS. In BORIS you can create projects in which you can code different observations. How many videos you can include in one observation highly depends on the hardware you are using. Commonly around 150 videos should be possible. It is recommended to create for each Bower a single project, as this helps with organising the data later on and for the sake of simplicity. You can also create your own ethogram with predetermined behaviours. We have prepared an ethogram which we can provide and this can be imported into the different projects (Table 2). These behaviours are the most seen behaviours. Additionally to the ethogram you can create a list of Individuals which will be likely present in the videos such as the Bower-owners and some known auxiliary males. It is recommended to only add Individuals beforehand that are known to be present at the bower and adapt the list of subjects as you are coding. Many videos won't show any bowerbirds; those videos have to be distinguished into two groups: The first group are videos where any other animals are present. For this group we have the "behaviour" "animal" in the ethogram. If you know the species you can write them in the commands section of the coded behaviour. The second group are videos were nothing is present those videos should be deleted and are therefore marked with the behaviour "delete". The Behaviours and subjects are assigned to different keys, which can be individually adapted.

The individuals are determined with the help of their colour bands. When the bird has lost some colour bands, name the column with the colour combination you see in the video. When an individual is unbanded create a subject "unbanded" to code it's behaviour. The same "unbanded" subject can be used from a video to the next even if this individual might not be the same. When an individual is banded but cannot be identified due to bad visibility etc. create a subject "unidentified" to code it's behaviour. The same "unidentified" subject can be used from a video to the next even if this individual might not be the same. If multiple "unbanded" or multiple "unidentified" birds are present in the same video, create multiple subjects for example "unidentified" and "unidentified_2" for the different behaviours that are shown. If a bird with missing bands and its original full colour combination cannot be guessed with certainty, then use his current colour combination to name the column. If a bird gets out of the of the frame while his bands were not visible and comes back within the same video with visible bands (and vice versa), then it has to be categorised with an unknown bird and a banded birds in the same video. However, in a similar situation, if the unknown bird had bands visible but not enough to be sure of his ID (for example one leg visible only) and then comes back with all bands visible, it can be categorised as a single individual. This last rule can apply also for two distinct videos that are following each other (less than one minute between the end of the first and the start of the second).

Use the notes function next to the coded behaviours to take notes of anything unusual that cannot be describe with codes and need to be mentioned.

Remember to save regularly and to make at least once a day a backup copy of the file on a different hard drive.

Table S 1: example for a list of subjects

	Key	Name	Description
1		No focal subject	
2	y	OWM-RSN	owner
3	v	unidentified	unid
4	x	BM-Y	old owner
5	c	EYM-EYS	?
6	b	BER-NYM	aux

Table S 2: list for categorisation codes and their meaning

	Behavior type	Key	Code	Description
1	Point event	1	absent or not visible	not visible or absent, or the present bird cannot be identify as this individual
2	Point event	2	present	present but do no engage in any activity
3	Point event	3	maintenance	moving and bringing material or decorations, clearing unwanted objects
4	Point event	4	painting	painting the walls of the bower with chewed leaves
5	Point event	5	display alone	producing a courtship display without any visible bird
6	Point event	6	display with other(s)	producing a courtship display with other bird(s) present, in or out the avenue
7	Point event	7	receive display	attending to a courtship display while standing in the bower avenue
8	Point event	8	destructing bower	destroying the bower, in any proportion
9	Point event	9	stealing decoration	stealing decoration (generally happens after a destruction)
10	Point event	0	interact with other species	interacting with an extra-specific animal, generally an intruding animal
11	Point event	ß	conspecific agonistic interaction	attacking or being attacked by another bowerbird (generally an intruder)
12	Point event	q	crouching/cloaca dilatation	crouching to indicate copulation acceptance and/or showing cloaca dilatation
13	Point event	w	copulation	copulating (receiving or mounting)
14	Point event	e	unknown beahvior	producing an unknown or a non-categorizable behaviour, put details in notes
15	Point event	a	animal	other animal than bower bird
16	Point event	d	delete	delete video as not useable
17	Point event	h	human	humans are present
18	Point event	k	clock	showing clock to the camera
19	Point event	f	feeding	Bird is feeding "mostly food provishining experiment"

Table S 3: example for list of observations

Events for "B68_HD1_BTCF_150" observation

	Time	Frame index	Subject	Code	Type	Modifier	Comment
1	00:00:00.000	6	YY-YM	absent or not visible			
2	00:00:02.100	126		delete			
3	00:00:31.750	90		animal			
4	00:00:55.917	340		animal			
5	00:01:12.750	135		animal			
6	00:01:32.900	129		animal			
7	00:01:52.583	95		animal			
8	00:02:59.750	2910	YY-YM	display alone			
9	00:03:10.383	3548	YY-YM	absent or not visible			

Vegetation survey analysis

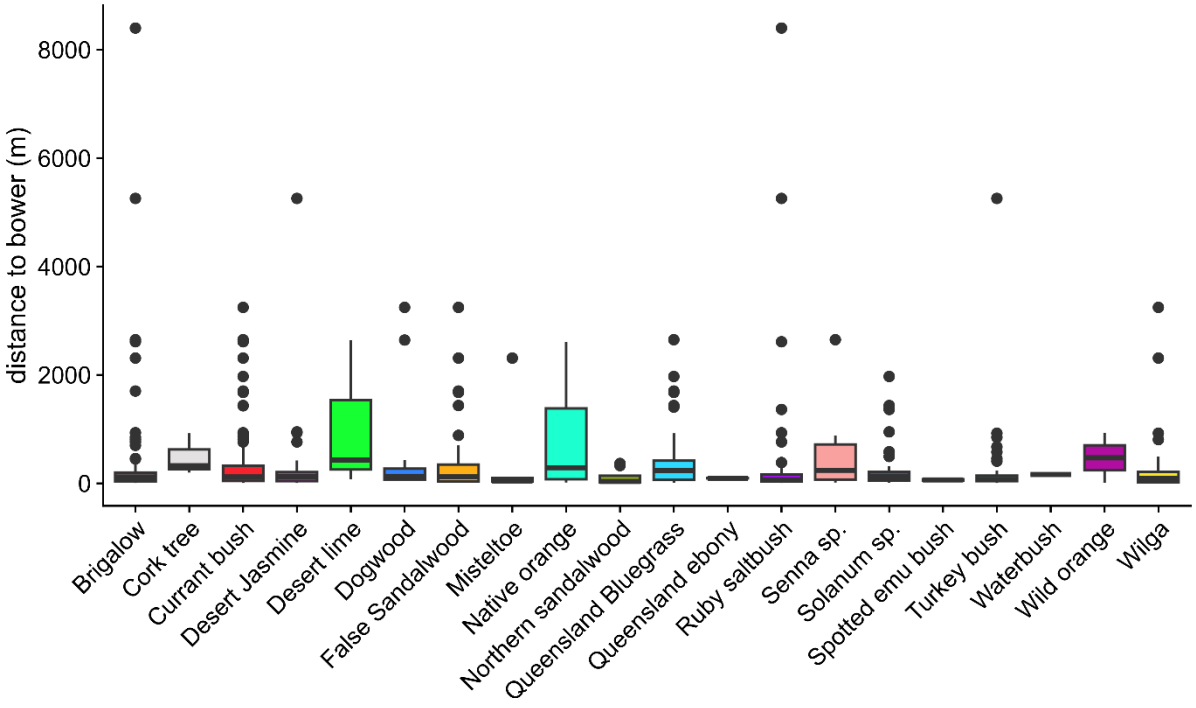

Figure S 1: Boxplots showing the variation in distance to the bower of all squares a species was present in

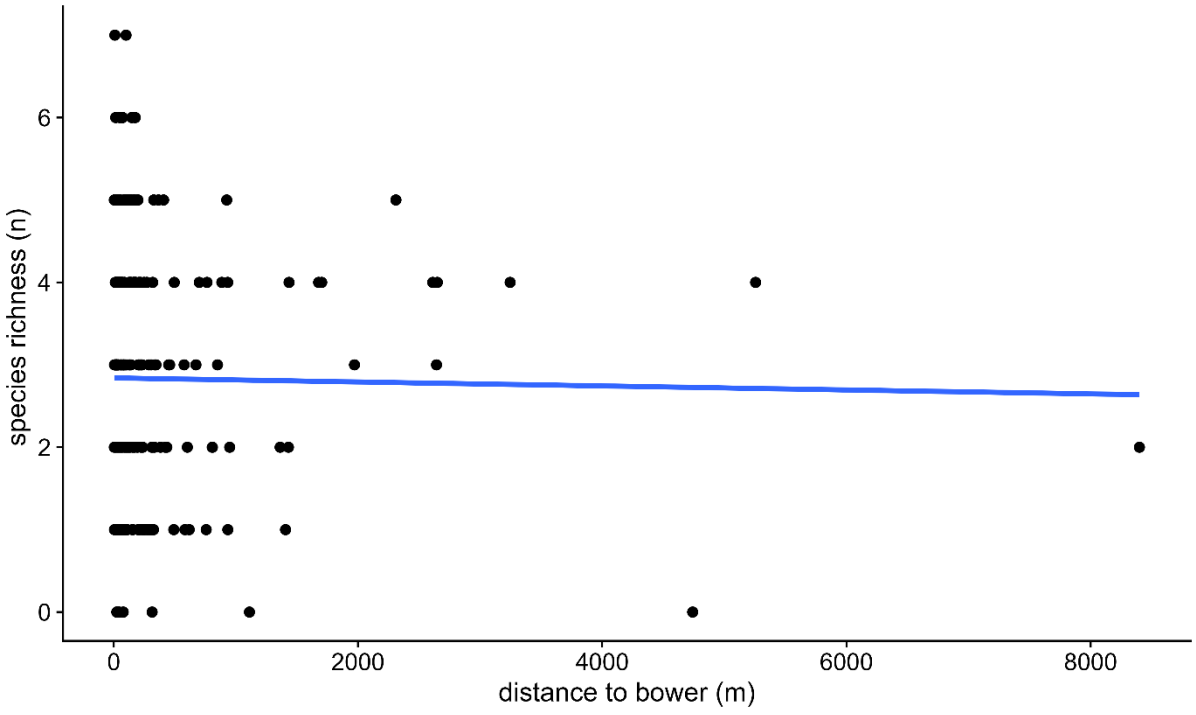

Figure S 2: shows a relation between the distance to the bower and the focal plant species richness of the squares

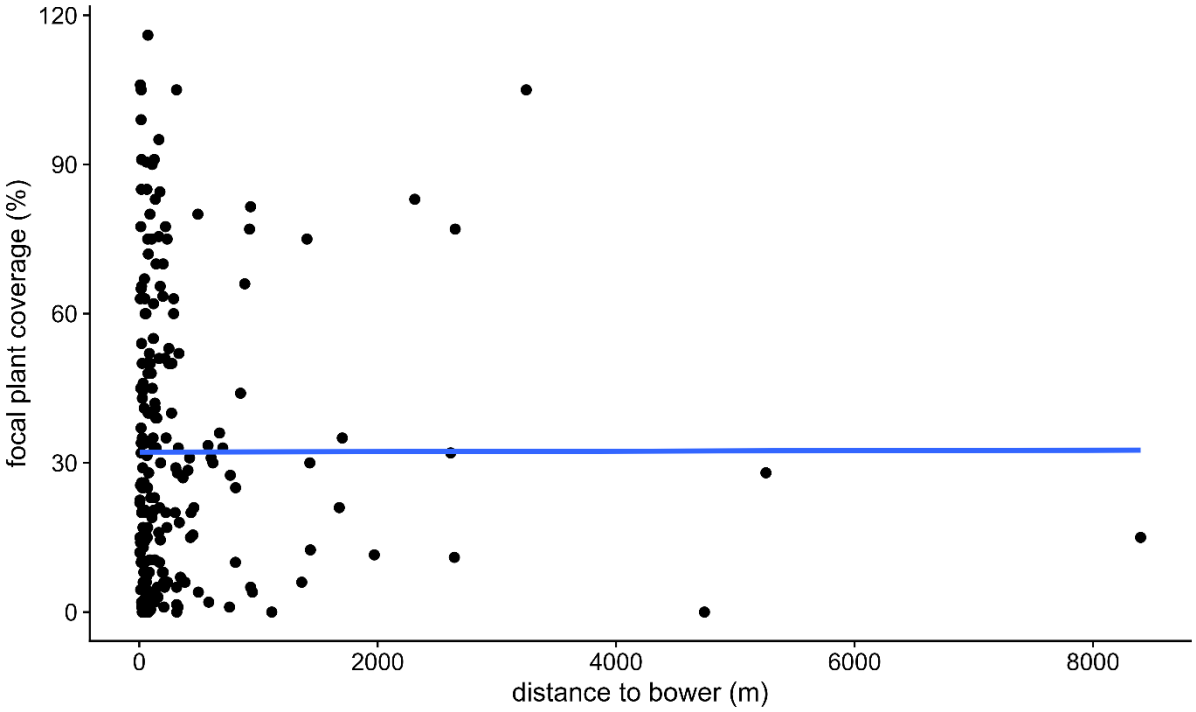

Figure S 3: shows a relation between the distance to the bower and the focal plants coverage.