

Nuptial gifts in a cooperative breeder

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1. ABSTRACT

Nuptial gift giving in general, and courtship feeding in particular, is a behaviour poised between sexual cooperation and sexual conflict: nuptial gifts can act as an indirect paternal investment into shared young between the sexes, or as part of the male's mating effort trying to ensure access to reproduction. Cooperative breeding, in which more than a pair of conspecifics cooperate to raise young, allows for group living and complex social structures, and thus provides an interesting context in which to study courtship feeding.

In this study, I explore courtship feeding behaviour in the cooperatively breeding bird *Malurus coronatus coronatus*. Specifically, I test two research questions. First, how does cooperative breeding affect courtship feeding – is there load-lightening for the dominant male, or increased cumulative investment in terms of courtship feeding for the dominant female, and what incentivizes subordinates to assist in courtship feeding? Second, what role does courtship feeding play - does it function as paternal investment or mating effort? These questions are addressed in three datasets: focal observations from 2020 as well as two long-term datasets from 2006 – 2009 and 2016 – 2020.

Dominant male courtship feeding effort was reduced in the presence of subordinates, and dominant females received fewer feeds with increasing subordinate number in 2006 – 2009 but not in 2016 – 2020. This indicates load-lightening for the dominant male, rather than increased investment in the dominant female, and may represent adaptive undercompensation or a cost of group living. Subordinates only fed the dominant female if they were related to the dominant male, indicating that they may engage in courtship feeding to support the dominant male's mating effort.

Both reproductive output (measured as nest abandonment, delay between finishing the nest and laying the first egg, clutch size, or number of fledglings) and copulation rate were not affected by courtship feeding – there is thus no direct evidence for courtship feeding acting as either paternal investment or mating effort. Indirect evidence for the mating effort hypothesis comes from the timing of courtship feeding, which is observed with greater frequency shortly before nest building starts, indicating that courtship feeding may act as an incentive for the dominant female to start a breeding attempt.

Overall, this project presents a first step towards understanding an interesting behaviour. However, several factors limit the explanatory power of this study. For example, it was not within the scope of this study to comprehensively test all hypotheses concerning why subordinates participate in feeding the dominant female, and strong observer effects may have obscured some patterns. Future experiments may be able to address some of these short comings, for example by investigating how their relatedness to the dominant female impacts whether the subordinate feeds, or whether group members plastically adjust their feeding rates to the feeding rates of other group members.

2. INTRODUCTION

Historically, the prevailing view of reproduction was one of harmonic cooperation between the sexes. More recently, this view was replaced by the concept of sexual conflict: differing evolutionary interests between males and females giving rise to antagonistic coevolution (Parker 1979, Chapman et al. 2003). Sexual conflict has proven to be widespread and is explored in a large body of both theoretical and empirical literature (reviewed for example in Chapman et al. 2003). Investigating the balance between cooperation and conflict in reproduction has proven to be a fruitful approach, with implications for a wide range of fields, including but not limited to life history evolution (Sexual conflict prevents the realization of sex-specific life-history optima, promoting mal-adaptive ageing rates beyond ageing as a cost of reproduction; Wedell et al. 2006, Bonduriansky et al. 2008, Aloise King et al. 2013), diversification (sexual conflict promotes ecological adaptation and diversification by allowing the exploration of a broader phenotypic space than viability selection as well as by providing pre-adaptations which first evolve as sexual trait and secondarily gain viability-related functions; Bonduriansky 2011, Gavrillets 2014), evolvability (sexual conflict facilitates increased mutation rates through strong sexual selection, which decreases mutational load and filters for rare beneficial mutations; Agrawal 2001, Siller 2001, Petrie & Roberst 2007), and speciation (sexual conflict may lead to antagonistic co-evolution between males and females, which can generate rapid divergence of traits involved in reproduction, thus facilitating sympatric speciation; Arnqvist et al. 2000, Gavrillets & Waxman 2002, Simmons 2018).

The behaviour of nuptial gift giving is poised between sexual conflict and sexual cooperation, making it an especially relevant phenomenon to study in this context. Nuptial gifts are defined as “materials beyond the obligatory gametes that are transferred from one sex to another during courtship or mating” (Lewis & South 2012) – usually passed from male to female, although sex reversals do occur (Lack 1940, Arnqvist et al. 2003, Lewis & South 2012). Nuptial gifts show great diversity, both in substance (ranging from prey items to pheromones or neuroendocrine modulators) and in mode of transfer (with oral or genital transfer being the most common) (Lewis & South 2012). The provision of edible, orally transferred and exogenous (i.e. not produced by the male himself) nuptial gifts are referred to as courtship feeding – in other words, courtship feeding is a type of nuptial gift giving in which an individual presents its mate with a food item (Lewis et al. 2014). Nuptial gifts in general and courtship feeding in particular are common across vertebrates and invertebrates alike (Lack 1940, Vahed 1998), with most studies so far focusing on birds or insects. Nuptial gifts have been studied since the early 20th century (Fabre 1917) and have long since been recognized as an important facet of sexual conflict and cooperation (Andersson 1994) – yet in comparison to other, more conspicuous sexually selected traits such as male ornamentation, nuptial gifts have received little attention in evolutionary research (Lewis & South 2012).

Considering the cost nuptial gifts impose on the donor (Lewis & South 2012), the question arises what evolutionary forces gave rise to this behaviour in the first place. Various explanations have been put forward, which can be broadly categorised into two contrasting hypotheses: the mating effort hypothesis (reflecting sexual conflict over mating opportunities) and the parental investment hypothesis (reflecting sexual cooperation in raising shared offspring) (Vahed 1998, Vahed 2007). The mating hypothesis postulates that nuptial gifts function as a form of mating effort, increasing the male’s access to reproduction by overcoming female resistance (Vahed 1998, Vahed 2007). Nuptial gifts as mating effort can act at any stage of the courtship process (Maxwell & Prokop 2018): valuable nuptial gifts may attract females in the first place, either with their direct nutritional benefits, or by indicating male quality (mate appraisal hypothesis; Helfenstein et al. 2003, Macedo-Rego et al. 2016). This attraction can also be manipulative in nature: some evidence suggests that an important if not

primary role of nuptial gifts is to exploit sensory biases in females to trick them into mating (sensory trap hypothesis; Sakaluk 2000, Stålhandske 2002, Vahed 2007). Next, nuptial gifts may facilitate copulations: nuptial gifts can act as a form of payment which the male provides in exchange for copulations – consistent with the observation that in some arthropods nuptial gifts increase the probability of a copulation taking place or are even a necessary prerequisite for a successful copulation (principal agent hypothesis, also known as “meat for sex”; Stålhandske 2001, Gao & Hua 2013, Roughgarden 2013). Finally, nuptial gifts may increase paternity share in competitive matings (paternity assurance hypothesis) via a variety of mechanisms: they can increase copulation duration or the rate of sperm transfer, thus providing an advantage in sperm competition (Stålhandske 2001, Gao et al. 2019), or they can contain anti-aphrodisiac compounds, thus reducing the probability of the female re-mating (Chapman 2001).

In contrast, the parental investment hypothesis postulates that nuptial gifts function as a form parental investment, increasing the male’s offspring’s fitness or number (Vahed 1998, Vahed 2007). The term ‘parental investment’, first introduced by Fisher, refers to “any investment by the parent in an individual offspring that increases the offspring's chance of surviving [...] at the cost of the parent's ability to invest in other offspring” (Trivers 1972, Engels & Sauer 2006). Nuptial gifts, especially nutritionally valuable nuptial gifts, can increase reproductive output by improving female condition (female nutrition hypothesis): nuptial gifts have been linked to increased quantity (Lamunyon 1997, Helfenstein et al. 2003, Engels & Sauer 2006) and quality (Reinhold 1999, García et al. 2011) of offspring. Alternatively, nuptial gifts may provide highly valuable compounds to the male donor’s offspring via the female, such as defensive alkaloids or sodium in species living on sodium-poor diets (Smedley & Eisner 1996, Lamunyon 1997, Bezzerides & Eisener 2002). Noteworthy is also that according to the parental investment hypothesis, males may not be able to ensure that their investments benefit exclusively their own offspring rather than all offspring of the female, regardless of their father (Bezzarides & Eisener 2002).

In this study, the question of what evolutionary pressures give rise to nuptial gift giving is addressed in the context of cooperative breeding. Cooperative breeding, in which more than a pair of conspecifics are involved in raising offspring (Koenig 2017), is wide-spread across birds and mammals, and – to some extent fish (for example Koenig & Dickinson 2004, Koenig & Dickinson 2016, Lukas & Clutton-Brock 2017). The reproducing pair are referred to as dominant individuals, the helpers as subordinate individuals. The dominants may benefit from the help provided by subordinates at various stages of the breeding cycle, including but not limited to help with nest-building, incubation, food provisioning, territory defense and defense against brood parasitism (see for example Komdeur 1994, Feeney et al. 2013, Quiñones et al. 2016). This help can result in increased lifetime reproductive output (Tanaka et al. 2018), via two routes: load-lightening or increased cumulative investment/differential allocation (Dixit et al. 2017). In the case of load-lightening, the dominant individuals reduce their effort – a reduction that is compensated for by the additional investment from the subordinates. This reduced effort allows the dominants to invest instead into self-maintenance, thus extending their lifespan and life-time reproductive success (Crick 1992, Russell et al. 2008, Hatchwell et al. 2014). Conversely, if the dominant individuals do not reduce their effort in the presence of helpers, the current offspring receive increased cumulative care (the unchanged care from the dominant individuals, i.e. their parents, plus the additional care from the subordinated helpers). This increased cumulative care may improve offspring quality and/or quantity (Hodge 2005), thus increasing reproductive output. In addition to this increased cumulative investment experienced by the offspring, the dominants may also increase their own investment in the offspring in the presence of helpers, if larger group sizes, for example, indicate good conditions (Savage et al. 2015). Subordinates, too, may benefit from cooperative breeding in various ways:

indirect fitness benefits of helping can be incurred if subordinates and dominants are related (Griffin & West 2003, Richardson et al. 2003), subordinates benefit from access to high quality territories (Komdeur et al. 1995), and by helping the dominants raise their offspring they can increase the group size which can in itself be beneficial (group augmentation, Heg et al. 2004, Garay & Varga 2011, Kingma et al. 2014). Finally, subordinates can gain indirect reproductive benefits if helping behaviour increases the chances of territory inheritance (Balshine-Earn et al., 1998), provides practice with important skills such as nest building (Komdeur 1996), or allows them obtain direct access to reproduction (e.g. by siring some of the offspring, Richardson et al. 2002). Overall, group living, and especially cooperative breeding, exhibit complex social dynamics and thus provide an interesting context in which to study nuptial gifts.

Study aims and study species

In this study, I will investigate what function nuptial gifts have in a facultatively cooperatively breeding species, as well as how cooperative breeding impact nuptial gift giving. The study species in this research project is the purple-crowned fairy wren, and specifically the subspecies *Malurus coronatus coronatus*. *M. coronatus* is a cooperative breeder, in which 40%-70% of pairs have on average one or two subordinates (Kingma et al. 2010, Kingma et al. 2011a). These subordinates can be male or female, related or unrelated group members (Kingma et al. 2011a), and help with food provisioning and predator defense (Kingma et al. 2010, Teunissen et al. 2020a, Teunissen et al. 2020b). They have been shown to benefit from this helping behaviour if they are related to the dominants (kin selection) or if they are likely to inherit the breeding position (active group augmentation: they benefit from inheriting a larger group) (Kingma et al. 2011a). *M. coronatus* occurs in the tropics of north-western Australia, in the Kimberly region, and breeds mostly during the wet season. In this region, the climate, especially rainfall and food abundance, is variable and often unpredictable (Shine & Brown 2008). Furthermore, they are riparian habitat specialists (Rowley 1993, Skroblin & Legge 2012) and dependent on vegetation containing *Pandanus* spp. (Skroblin & Legge 2012). Their habitat is threatened by fragmentation and degradation, especially through introduced herbivores and wildfires (Skroblin & Legge 2012), and the Western subspecies *Malurus coronatus coronatus* (the focus of this study) is endangered (Garnett et al. 2011). *M. coronatus* also provides an interesting species in which to study sexual conflict: previous studies have shown that the levels of extra-pair paternity are overall low (Kingma et al. 2009), yet males do exhibit intense mate-guarding (Hall & Peters 2009), which suggests that paternity assurance does indeed play an important role in this species. Finally, the dominant male as well the subordinates have been shown to feed the dominant female (Hall & Peters 2009). To sum up, *Malurus coronatus coronatus* is a species well suited for investigating the function of nuptial gifts and the impact of cooperative breeding on nuptial gift giving: They are a cooperative breeder with easily observable nuptial gifts, in which the pre-requisite of the mating effort hypothesis (potential conflict over access to paternity, as evidenced by female choice, extra-pair paternity and mate-guarding) as well as the prerequisite of the parental investment hypothesis (a harsh environment in which extra food items are likely to be valuable) are both fulfilled.

Research approach

This project is split into two research questions. Firstly, I will look at how cooperative breeding influences nuptial courtship feeding. In my first hypothesis for this research question (Hypothesis 1a) I suggest that there is load-lightening for the dominant male in the presence of subordinates. As the presence of subordinates, and thus the courtship feeds provided by subordinates, increases, the dominant male can reduce his effort and provide fewer courtship feeds to the dominant female. The dominant female hence does not receive more courtship feeds in the presence of more subordinates. In this scenario, the dominant male benefits from the presence of subordinates, as he

can reduce his workload. In my second hypothesis (Hypothesis 1b) I suggest that, in the presence of subordinates, the dominant female receives a higher number of courtship feeds: if the dominant male does not reduce his courtship feeding effort in the presence of subordinates, the dominant female receives more food items as the number of subordinates increases. In this scenario, the dominant female benefits from the presence of subordinates. Hypothesis 1a and 1b are not mutually incompatible— the dominant male might, for example, reduce his courtship feeding effort only partially, thus allowing a partially reduced workload for himself as well as increased cumulative investment for the dominant female. Additionally, the question arises why subordinates help with courtship feeding in the first place: does their investment into courtship feeding reflect investment into the offspring (Hypothesis 1c), or are they assisting the dominant male in assuring his paternity (Hypothesis 1d)? Hypothesis 1c predicts that subordinates help irrespective of their relatedness to the dominant male: related subordinates benefit from investment into the young via kin-selection, and unrelated subordinates benefit through investment into future group members due to group augmentation advantages such as improved defense against predators (Teunissen et al. 2020b) or, for male subordinates, the chance to inherit a larger, more productive group after the death of the male (Kingma et al. 2011a). Hypothesis 1d predicts that subordinates related to the dominant male engage more in courtship feeding, as only these subordinates related to the dominant male have an interest in assuring paternity for him. Relatedness of subordinates to the dominant female is not considered in this study, as the predictions for this variable are less clear.

The second research question concerns the role of courtship feeding: does it function as parental investment (Hypothesis 2a) or as mating effort (Hypothesis 2b)? In other words, in the second research question I will explore which of the two roles of courtship feeding discussed above hold true. To do so, I will investigate several variables (see table 1): If courtship feeding is a type of parental investment (Hypothesis 2a), I predict increased reproductive output from reproductive events in which the dominant female was fed more; specifically I predict decreased nest abandonment prior to egg laying, a decreased delay between finishing the nest and laying the first egg, a greater clutch size and more live fledglings if the dominant female was fed more. The rate of copulations, specifically the interest that the female has in copulations (success of the copulation attempt notwithstanding) is predicted to be unaffected by the rate of courtship feeding. The next prediction concerns the timing of courtship feeding: If acting as parental investment, courtship feeding should increase after the female has started building the nest, i.e. once there is indication that there will soon be offspring which will receive current paternal investments. Furthermore there is no reason to expect the rate of courtship feeding to be predicted by the rate of paternity assurance mechanisms such as physical mate guarding. The next variable of interest is territory quality: I predict that if courtship feeding functions as parental investment, dominant females will receive more courtship feeds in low quality territories. Feeding offspring post-hatching in low quality territories poses a greater difficulty, so investment into the offspring before egg-laying (which may offset some of the later difficulties in feeding) are of greater importance. Conversely, if courtship feeding functions as mating effort rather than parental investment, I predict no increase in reproductive output (i.e. nest abandonment prior to egg laying, the delay between finishing the nest and laying the first egg, the clutch size and the number of live fledglings are not affected by the courtship feeding rate). The rate of copulations, specifically the interest that the female has in copulations, increases with the courtship feeding rate. Predictions regarding the timing of courtship feeding depend on the mechanism by which courtship feeding improves mating effort. Courtship feeding might occur with increased frequency prior to the start of a reproductive attempt (i.e. prior to nest building), acting as an incentive for the female to start the reproductive attempt. In this case, courtship feeding acts as mating effort by facilitating the reproductive event in the first place (principal agent hypothesis or meat for sex hypothesis, cf. above). Alternatively, courtship feeding may act as mating effort by assuring paternity during a reproductive event (paternity assurance hypothesis, cf. above) – in that case, the rate of courtship feeding should be predicted by the rate of

physical mate guarding, since both behaviours fulfill the same function. Depending on the duration of the breeding attempt, the two predictions regarding timing may be incompatible with one another: mate guarding peaks 3 days prior to egg laying (Hall & Peters 2009) which in all but extremely rapid breeding attempts is after nest building has started. Territory quality should not affect the rate of courtship feeding, since males in both high and low quality territories have similar interest in obtaining matings. A summary of the predictions can be found in Table 1.

Table 1: This table lists the predictions for the two contrasting hypotheses on the role of courtship feeding: courtship feeding as parental investment, and courtship feeding as mating effort. Throughout the table, 'CF' is used as abbreviation for courtship feeding.

	Reproductive output				Copulation rate	Temporal patterns	Spatial patterns
	Abandonment Yes/No	Delay to 1 st egg	Clutch size	Live fledglings			
Hypothesis 2a: Parental investment	↑ CF = ↓ abandonment	↑ CF = ↓ delay	↑ CF = ↑ clutch size	↑ CF = ↑ Nr. of fledglings	No effect of CF	Peak CF after nest building begins; no relation to physical mate guarding	More CF in low quality territories
Hypothesis 2b: Mating effort	No effect of CF				↑ CF = more copulations	Peak CF early in the reproductive cycle; and/or peak CF = peak physical mate-guarding	Territory quality does not affect CF

3. METHODS

The research questions detailed above are explored in three datasets. The first dataset consists of data I collected myself at the beginning of this project. However, the *Malurus coronatus coronatus* population at the study site underwent a severe population crash in the past two years reducing the number of subordinates, and thus the sample size, considerably. The sample size was further impacted by my unexpectedly early departure from the research site due to the Covid-19 pandemic. To compensate for the smaller dataset, I also extracted data from two long-term databases, based on data collected between 2006 and 2009 (the second dataset) and data collected between 2016 and 2020 (the third dataset).

3.1 General information regarding data collection

All three datasets are based on observations of the *M. coronatus coronatus* population at Mornington, Western Australia. The fully ringed study population inhabits the vegetation along Annie Creek, a small river with seasonal water flow. Throughout, only non-dominant individuals over the age of 90 days were counted as subordinates, below that age they were regarded as fledglings. As measure of relatedness social relatedness, rather than genetic relatedness, is used, which is sufficiently accurate due to the low level of extra pair paternity (Kingma et al. 2009). In all datasets,

the outcome of breeding attempts was recorded when possible – here, the number of live fledglings was treated as unknown if the young died as a result of predation during the egg or nestling stage, since the probability of predation is presumably mostly independent of parental quality and is thus deemed not affected by parental investment.

3.2 Data collected systematically in the breeding season 2020

All observations for this dataset were carried out in February and March 2020, between 5am and 12am during the nest building stage, i.e. during peak nest building activity, with one or two observations per morning. Observations were stopped one full day prior to the onset of egg laying at the latest. For each observation I followed the dominant female, for a cumulative though not continuous 42 to 100 minutes (mean = 110.1, standard error = 7.1), recording data every 30 seconds. If the female had not been in view for the entire preceding 30 seconds this did not count towards the observation length.

The following data was recorded: how often did any bird offer the dominant female food in the preceding 30 seconds, and did the dominant female accept the food? Did the dominant female solicit a copulation, and did a successful copulation take place? The identity (colour ring combination) of all birds involved in a behaviour was recorded as well. In addition to this, the progress of each nest was monitored, providing data on the nest stage (early vs. late stage) during the observation, nest abandonment, the delay between completing the nest and laying the first egg (measured in days, with a maximum of 10 days – the value 10 thus denotes delays of 10 days or more, and includes cases in which the nest was abandoned and a new nest had to be built prior to egg laying), the final clutch size, and total number of live fledglings produced (discounting parasitic brush cuckoo fledglings). Due to predation and flooding, the final clutch size and nestling weight are not known for all observed nests.

3.3 Data extracted from the long-term database

3.3.1 Data from 2006 - 2009

This database was compiled as part of a research project lead by Dr. Michelle Hall (Hall & Peters 2009). During the observations, which were carried out year-round, the dominant female was followed for ca. 60 min (the exact observation length is known), with a focus on recording physical mate-guarding. Other behaviours were also recorded, including courtship feeding (how often the dominant female was fed during the observation and by whom). The nest stage at the time of the observation was not recorded. The same female was frequently followed several times, even whilst still building the same nest. Regular nest monitoring provided information on the nest outcome: nest abandonment, clutch size, and the number of fledglings (except for cases in which the nest was not found, too high to monitor, or washed away by flooding before the outcome could be determined; such nests were excluded from analyses pertaining to nest outcome).

Data extraction:

I extracted all observations that were carried out during the nest building stage (i.e. excluding observations in the incubation phase or during the non-reproductive phase), for which the duration of the observation is known. In contrast to the data I collected systematically in the breeding season 2020, no distinction can be made between food offered and food accepted, since instances of food offered but not accepted are not recorded. Physical mate guarding is here defined as the dominant male being within 0.5 meters of the dominant female. Since observations were carried out year round, I also recorded whether observations took place during the dry season (April - November) or during the wet season (December - March). For analyses concerning the nest outcome (i.e. clutch size, etc.), all observations at one nest have to be combined into one. To do so, I added up the

duration of all observations at a single nest as well as the number of courtship feeds recorded during these observations. Overall, I extracted 127 observations from this database, from 8 different observers, 44 individual dominant females and 56 known individual nests.

3.3.2 Data from 2016 - 2020

This the database was compiled as part of the long-term *M. coronatus coronatus* population monitoring carried out by Monash University, led by Dr. Niki Teunissen who trained all other observers during this time period. The compilation of this database shows several differences to the compilation of the earlier database in 2006 - 2009, the most striking of which is that dominant females were followed with the express purpose of finding their nest - other behaviours were recorded opportunistically. Furthermore, a dominant female building the same (known, already found) nest was rarely followed more than once, the nest stage at the time of observation was recorded if known, all observations are carried out in the wet season, and the duration of the observation ranges from less than a minute to 89 minutes. As in the earlier database, regular nest monitoring provides information on the nest outcome: nest abandonment, clutch size, and the number of fledglings (except for cases in which the nest was not found, too high to monitor, or washed away by flooding before the outcome could be determined; such nests were excluded from analyses pertaining to nest outcome). However, a slightly different formula was used to calculate *Pandanus* volume, resulting in different scales of territory quality for data from the focal observations in 2020 and data from the long-term database.

Data Extraction:

I extracted all observations that were carried out during the nest building stage (i.e. excluding observations in the incubation phase or during the non-reproductive phase), during which courtship feeding behaviour was recorded and for which the duration of the observation is known and at least five minutes. In contrast to the data I collected systematically in the breeding season 2020, no distinction can be made between food offered and food accepted, since instances of food offered but not accepted are not recorded. As in the data I collected systematically and the data extracted for the years 2006 - 2009, I defined subordinates to be non-dominant individuals over the age of 90 days, relatedness to be social relatedness and the number of live *M. coronatus coronatus* fledglings to be unknown in the case of predation. For analyses concerning the nest outcome (i.e. clutch size, etc.), all observations at one nest have to be combined into one. To do so, I added up the duration of all observations at a single nest as well as the number of courtship feeds recorded during these observations. Overall, I extracted 417 observations from this database, from 7 different observers, 87 individual dominant females and 235 known individual nests.

3.4 Territory quality

The volume of *Pandanus* growth serves as a proxy for habitat quality, as *M. coronatus coronatus* has been shown to prefer territories with greater *Pandanus* cover (Kingma 2011b, Hidalgo Aranzamendi et al. 2016). In the breeding season in 2020, the level of *Pandanus* growth was assessed in the following way: *M. coronatus coronatus* territories are distributed linearly along Annie Creek. *Pandanus* growth is thus measured at fixed GPS points at regular intervals of 25 meters along Annie Creek. At each GPS point, the observer scored the following parameters for a stretch of 10 meters upstream and downstream of the GPS point: percentage of total length covered by pandanus, average depth of pandanus growth in meters, and height of pandanus growth (percentage of crowns which are over 3 meters tall). East and west bank were assessed separately, and only green foliage was taken into account. These measures of length, depth and height were then used to calculate *Pandanus* volume per GPS point. To estimate the quality of *Pandanus* growth per territory, the average of the *Pandanus* volume at each GPS point within the territory is taken.

In the long-term database, the quality of *Pandanus* growth is measured in a slightly different way: instead of estimating *Pandanus* volume, *Pandanus* growth is assessed by assigning scores between 0 (absence) and 20 (extremely dense and high growth) are assigned. Again, all scores within a territory are then averaged to give the territory quality score, however, GPS points in 2005 – 2017 were 50 meters apart rather than 25 meters, resulting in lower resolution. In years in which *Pandanus* growth was not quantified (2009 and 2016), the missing values were interpolated from the closest field measurements with the assumption that change in territory quality follows a linear trend.

3.5 Statistical analysis

Histograms of all variables were visually inspected to determine their distribution. For all models, model diagnostics and qq-plots were used to check model behaviour. All continuous explanatory variables were scaled and centered. All statistical analyses were carried out in R (version 1.2.1335, RStudio Team 2018). For the full output of the statistical models, see the appendix.

3.5.1 Dataset 1

As proxy for courtship feeds received and for dominant male courtship feeding effort I used the rate of courtship feeding, i.e. the number of times the dominant female received food during the observation (or the number of times the dominant male offered the dominant female food) divided by the length of the observation. A linear model was used for continuous response variables (courtship feeding rate, dominant male effort, copulation rate, delay between finishing the nest and laying the first egg) and a generalized linear model was used for the binary response variable (nest abandonment). In not abandoned nests, clutch size (with one exception) and the number of live fledglings were invariant (clutch size: mean = 2.88, SE = 0.13; number of fledglings: mean = 0, SE = 0), and thus did not show sufficient variation for a statistical analysis. In models analysing what influences the courtship feeding rate, number of subordinates, nest stage, territory quality and date were included as explanatory variables; in models analysing the consequences of courtship feeding, courtship feeding rate, nest stage and date were included as explanatory variables.

3.5.2 Dataset 2 and 3

In these data, possibly owing to the many short observations, a large proportion of observations did not show any instances of courtship feeding. Therefore, I used the binary presence or absence of courtship feeds during the observation as dependent variable. To control for observation duration, this variable was included as a covariate in the statistical models. Linear mixed effect models were used for continuous response variables (clutch size, the number of live fledglings) and generalized linear mixed effects models (family: binomial) for binary response variables (Whether or not the dominant female was fed by any group member, whether the subordinate bird fed the dominant female, nest abandonment). Observer, date, and identity of the dominant female were included as random effects when possible. If the model failed to converge, the random effect causing the lack of convergence was removed; in all such cases I confirmed that this did not qualitatively affect model output. Random effects that explained zero variance were removed.

4. RESULTS

4.1 Research question 1: Courtship feeding in the context of cooperative breeding

In the data I collected systematically through focal observations in the breeding season 2020, the dominant male offered the dominant female food significantly less often in the presence of a subordinate ($p = 0.043$, $t = -2.205$, estimate = -2.610, SE = 1.184; see Figure 1). No data is available in the other two datasets on the courtship feeding effort of the dominant male. There is a trend for the

dominant female to receive fewer courtship feeds when living in a group with a subordinate rather than a pair in dataset 1 ($p = 0.067$, $t = -1.972$, estimate = -2.171 , $SE = 1.101$; see Figure 2A), and the dominant female was fed during significantly fewer observations as the number of subordinates in the group increases in the data I extracted from 2006 to 2009 ($p = 0.039$, $z = -2.067$, estimate = -0.669 , $SE = 0.324$; see Figure 2B), but not 2016 to 2020 ($p = 0.650$, $z = -0.454$, estimate = -0.071 , $SE = 0.156$, see Figure 2C).

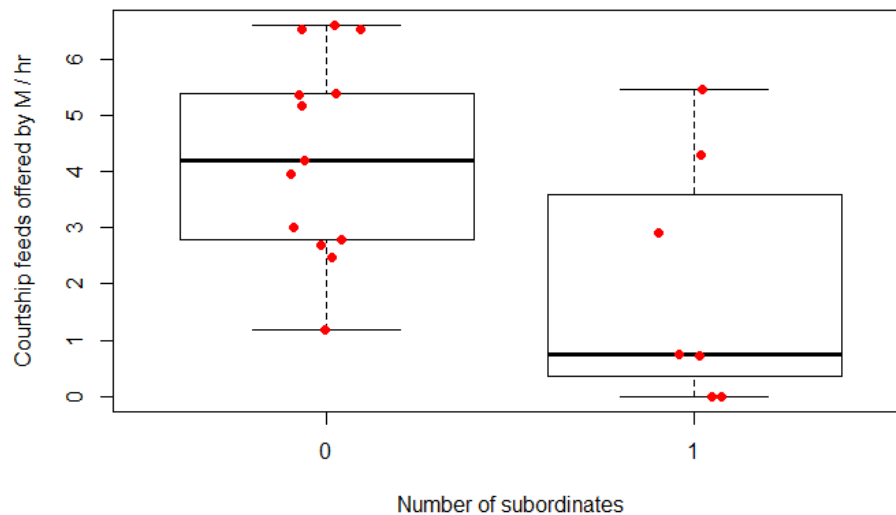


Figure 1: Effort put into courtship feeding by the dominant male (per hour) in groups with or without subordinates in the focal observations in 2020. The dominant male offered the dominant female significantly more food items per hour in the absence of subordinates. In this dataset, the maximal number of subordinates per group is one. Individual datapoints are shown in red.

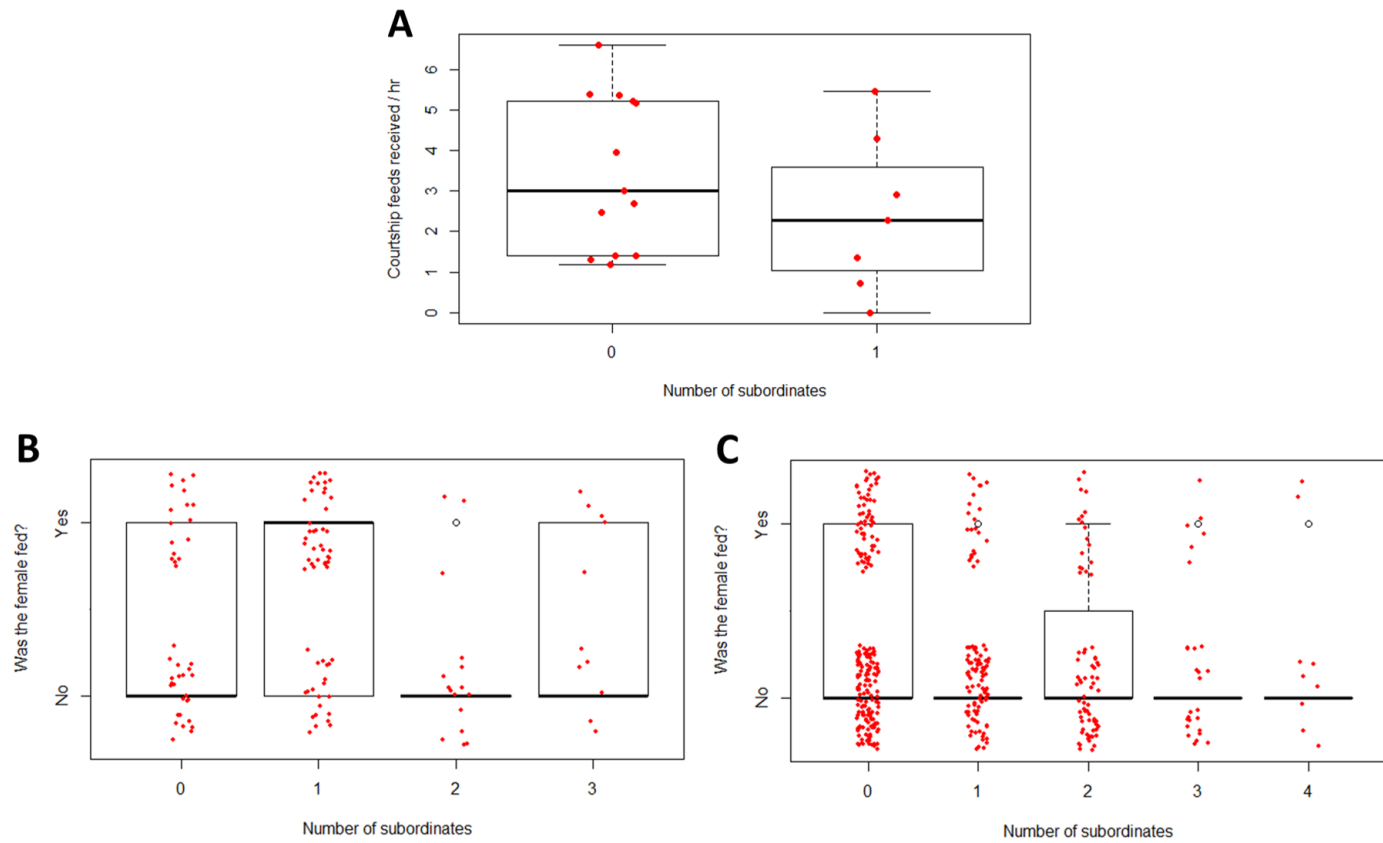


Figure 2: The impact of group size on courtship feeding. There is a trend for the dominant female to receive more food items per hour in the absence of subordinates in the focal observations in 2020, this trend is close to significant (Figure 2A), and the dominant female was fed in more of those observations that were carried out in groups with fewer or no subordinates in 2006 – 2009 (Figure 2B) but not in 2016 – 2020 (Figure 2C). Individual datapoints are shown in red, and are scattered around the values of 'Yes' and 'No' on the y-axis for easier visibility in Figures 2B and 2C.

In the data I extracted from 2006 – 2009 and from 2016 – 2020 combined, only subordinates related to the dominant male fed the dominant female (see Figure 3). This complete separation of data made the statistical analysis problematic. I thus carried out two different statistical tests: a generalized linear mixed effects model ($p < 0.001$, $z = 5.551$, estimate = 12.092, SE = 2.179; identity of the female as random effect), which did not fully converge, and Fisher's exact test ($p = 0.057$).

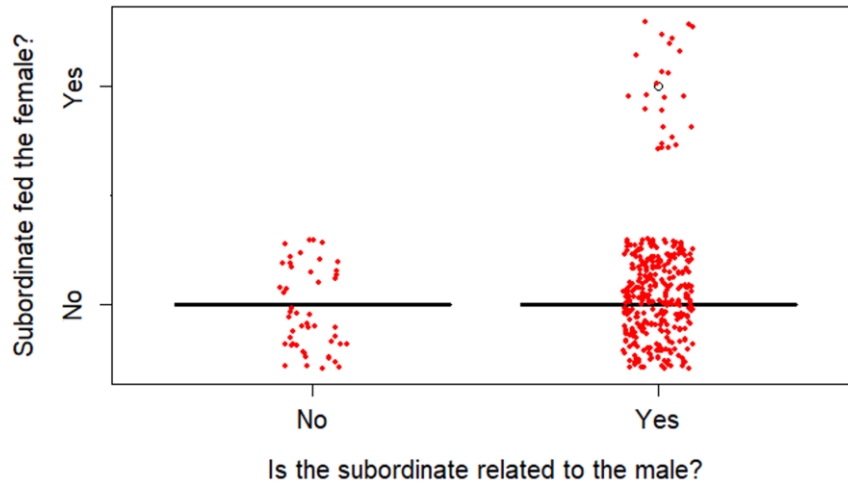


Figure 3: In 2006 – 2009 and 2016 – 2020, the 25 subordinates which were observed feeding the dominant female were all related to the dominant male (out of 349 subordinates related to the dominant male). Individual datapoints are shown in red, and are scattered around the values of 'Yes' and 'No' on the y-axis for easier visibility.

4.2 Research question 2: The role of courtship feeding

a) Abandonment

The rate at which the dominant female was fed did not significantly impact nest abandonment in the focal observations in 2020 ($p = 0.759$, $z = -0.307$, estimate = - 0.109, SE = 0.357; see Figure 4A). Nest abandonment was not significantly impacted by whether the dominant female was fed during the observation in the data I extracted from 2006 – 2009 ($p = 0.350$, $z = -0.934$, estimate = - 0.830, SE = 0.889; see Figure 4B), or in the data I extracted from 2016 – 2020 ($p = 0.557$, $z = 0.587$, estimate = 0.231, SE = 0.394; see Figure 4C).

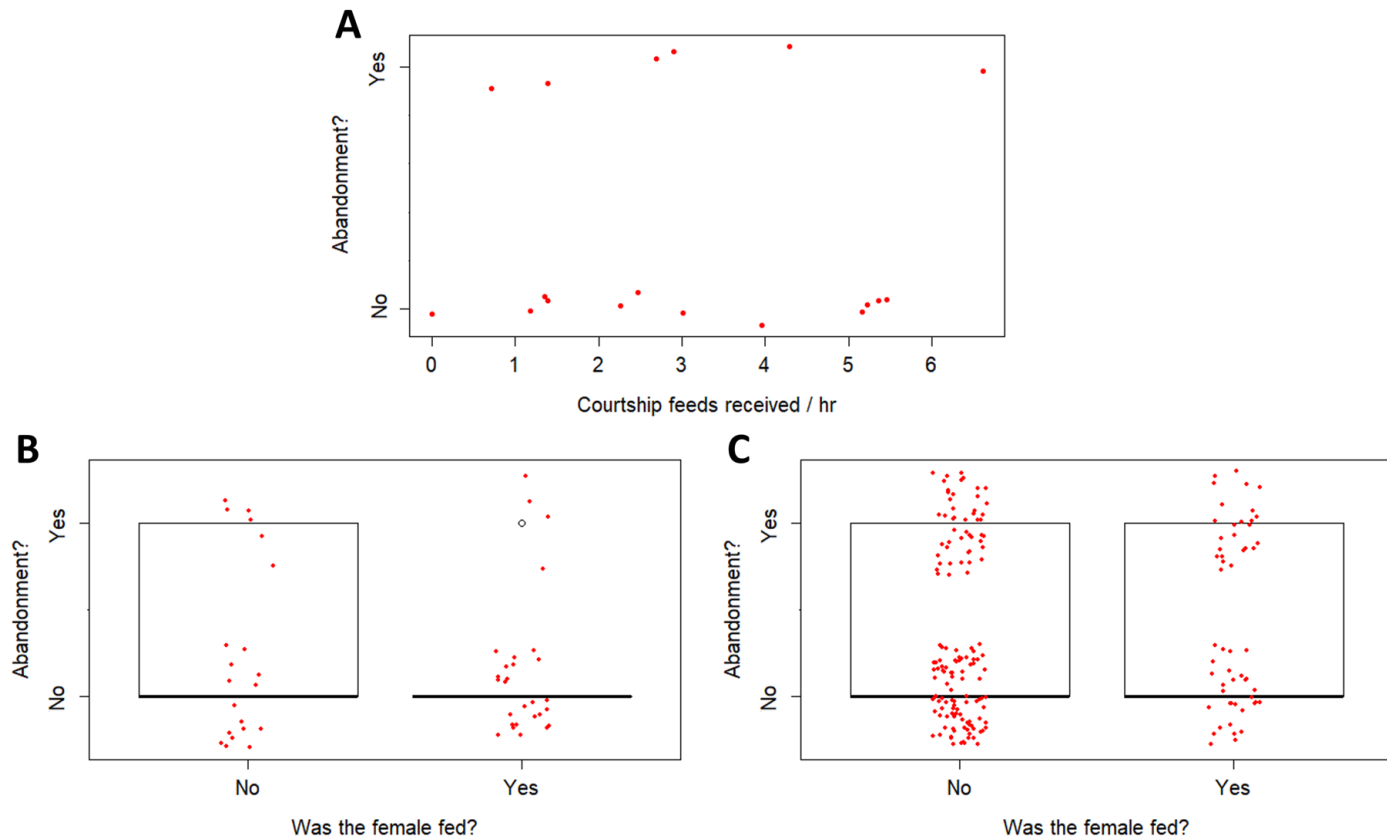


Figure 4: The impact of courtship feeding on nest abandonment. Courtship feeding did not impact abandonment in the focal observations in 2020 (Figure 4A), in the extracted data 2006 – 2009 (Figure 4B) or in the extracted data 2016 – 2020 (Figure 4C). Individual datapoints are shown in red, and are scattered around the values of 'Yes' and 'No' on the y-axis for easier visibility.

b) Delay between finishing the nest and laying the first egg

The rate at which the dominant female was fed did not significantly impact the delay between finishing the nest and laying the first egg in the focal observations in 2020 ($p = 0.510$, $t = -0.675$, estimate = -0.347 , $SE = 0.514$; see Figure 5). No data concerning this variable is available in the other two datasets.

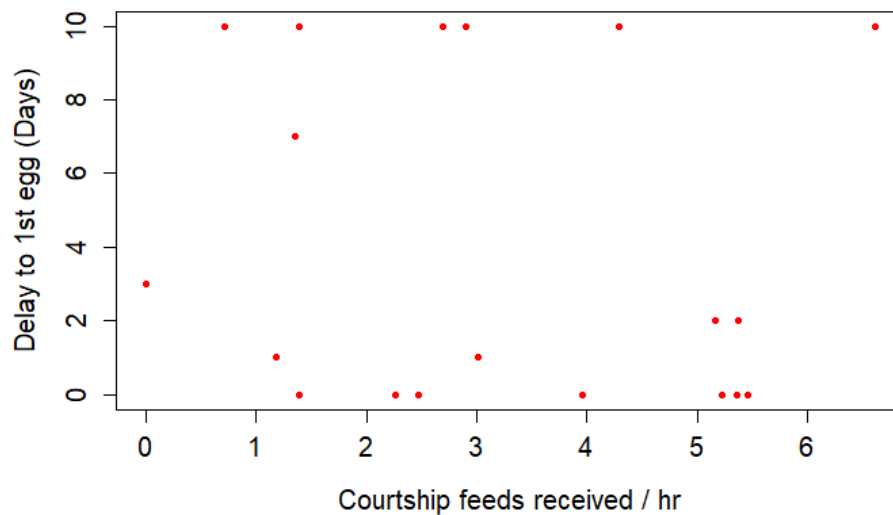


Figure 5: The impact of courtship feeding on nest abandonment on the delay between finishing the nest and laying the first egg, in the focal observations in 2020. The courtship feeding rate did not affect the delay between finishing the nest and laying the first egg. Individual datapoints are shown in red.

c) Clutch size

Clutch size was not significantly impacted by whether the dominant female was fed during the observation in the data I extracted from 2006 – 2009 ($p = 0.921$, $t = 0.100$, estimate = 0.036, SE = 0.362; see Figure 6A), or in the data I extracted from 2016 – 2020 ($p = 0.136$, $t = -1.505$, estimate = -0.195, SE = 0.129; see Figure 6B). No sufficient data concerning this variable is available in the focal observations in 2020.

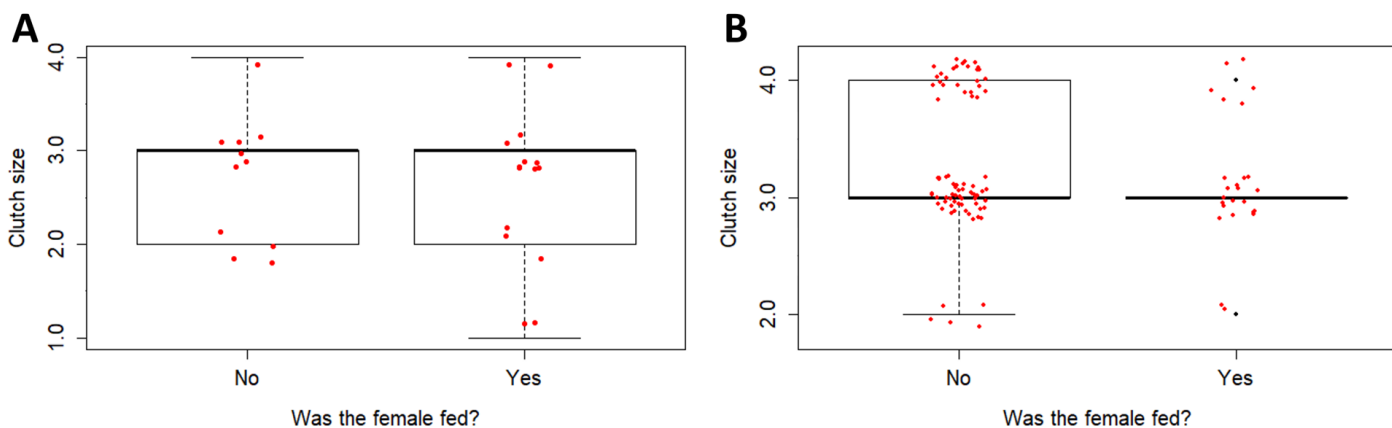


Figure 6: The impact of courtship feeding on clutch size. Courtship feeding did not impact clutch size in the extracted data 2006 – 2009 (Figure 6A) or in the extracted data 2016 – 2020 (Figure 6B). Individual datapoints are shown in red, and are scattered around the integer values for easier visibility.

d) Number of live *M. coronatus coronatus* fledglings

The number of live *M. coronatus coronatus* fledglings was not significantly impacted by whether the dominant female was fed during the observation in the data I extracted from 2016 – 2020 ($p = 0.518$,

$t = -0.651$, estimate = -0.276 , SE = 0.423 ; see Figure 7). No sufficient data concerning this variable is available in the other two datasets.



Figure 72: The impact of courtship feeding on the number of live *M. coronatus coronatus* fledglings, in the years 2016–2020. The presence or absence of courtship feeding did not affect the number of live *M. coronatus coronatus* fledglings. Individual datapoints are shown in red, and are scattered around integer values on the y-axis for easier visibility.

e) Female interest in copulation

The rate at which the dominant female was fed did not significantly impact whether the dominant female showed interest in copulation during the observation (i.e. whether a successful copulation took place or the dominant female solicited a copulation, successful or not) in the focal observations in 2020 ($p = 0.220$, $t = -1.294$, estimate = -0.247 , $SE = 0.191$; see Figure 8). No sufficient data concerning this variable is available in the other two datasets.

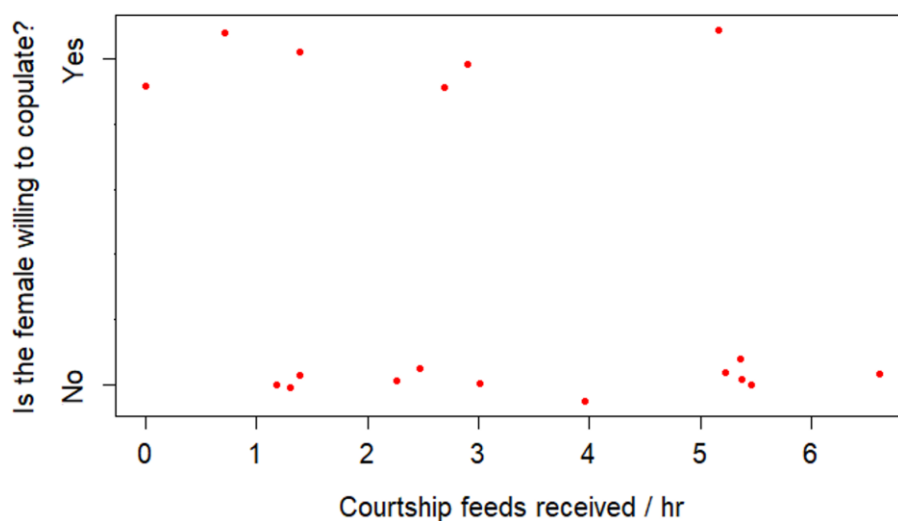


Figure 8: The impact of courtship feeding on the willingness of the dominant female to copulate with the dominant male in the focal observations in 2020. The courtship feeding rate did not affect the willingness of the dominant female to copulate.

Individual datapoints are shown in red, and are scattered around the values of 'Yes' and 'No' on the y-axis for easier visibility.

f) Timing of courtship feeding relative to nest stage

In the data I extracted from 2016 – 2020, the dominant female was fed during significantly more of those observations that took place before nest building started, as opposed to observations carried out during early stages of nest building ($p < 0.001$, $z = -3.459$, estimate = - 2.046, SE = 0.592; see Figure 9) and observations carried out during late stages of nest building ($p = 0.012$, $z = -2.507$, estimate = - 1.606, SE = 0.640; see Figure 9). No data concerning this variable is available in the other two datasets.

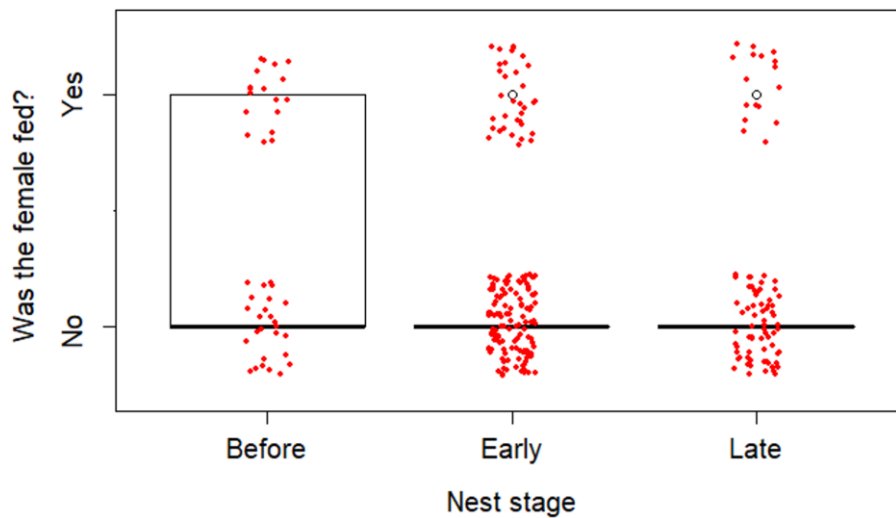


Figure 9: Presence or absence of courtship feeding during observations carried out before nest building, during the early stages of nest building, or during the late stages of nest building, in the years 2016 – 2020. The dominant female was fed during more of those observations which were carried out before nest building. Individual datapoints are shown in red, and are scattered around the values of 'Yes' and 'No' on the y-axis for easier visibility.

g) Timing of courtship feeding relative to mate guarding

In the data I extracted from 2006 – 2009, there is a trend for the dominant female to be fed during more of those observations which show higher physical mate guarding intensity (i.e. more time spent mate guarding by the dominant male; $p = 0.065$, $z = 1.847$, estimate = 0.514, SE = 0.278; see Figure 10). No data concerning this variable is available in the other two datasets.

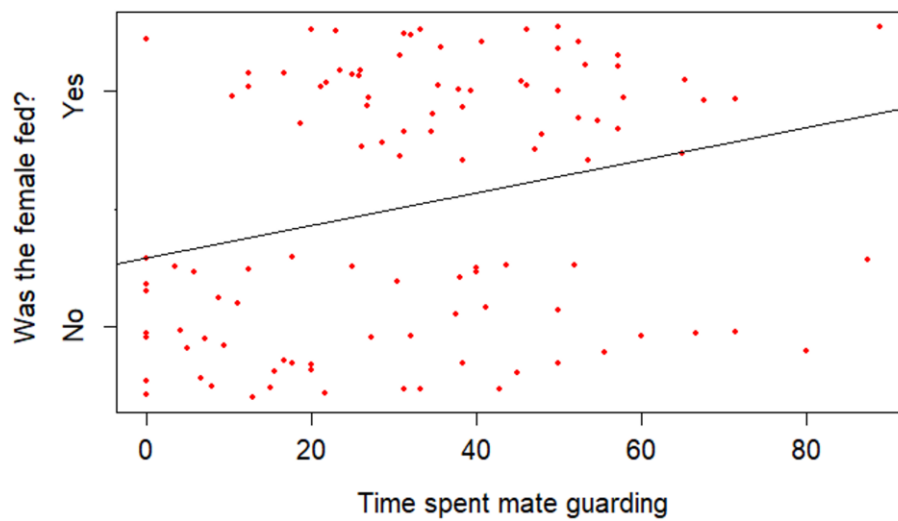


Figure 10: Presence or absence of courtship feeding during observations with different levels of physical mate guarding intensity in the years 2006 – 2009. There is a trend for the dominant female to be fed during more of those observations which show higher physical mate guarding intensity. Individual datapoints are shown in red, and are scattered around the values of 'Yes' and 'No' on the y-axis for easier visibility. A line of best fit is shown in black.

h) Territory quality

In the focal observations in 2020, the courtship feeding rate was significantly higher in higher quality territories ($p = 0.049$, $t = 2.144$, estimate = 0.013, SE = 0.006; see Figure 11A). In the data I extracted from 2006 – 2009, the dominant female was fed during significantly more of those observations carried out in lower quality territories ($p = 0.004$, $z = -2.851$, estimate = - 0.969, SE = 0.340; see Figure 11B). In the data I extracted from 2016 – 2020, the dominant female was fed during significantly more of those observations carried out in higher quality territories ($p = 0.002$, $z = 3.100$, estimate = 0.489, SE = 0.158; see Figure 11C).

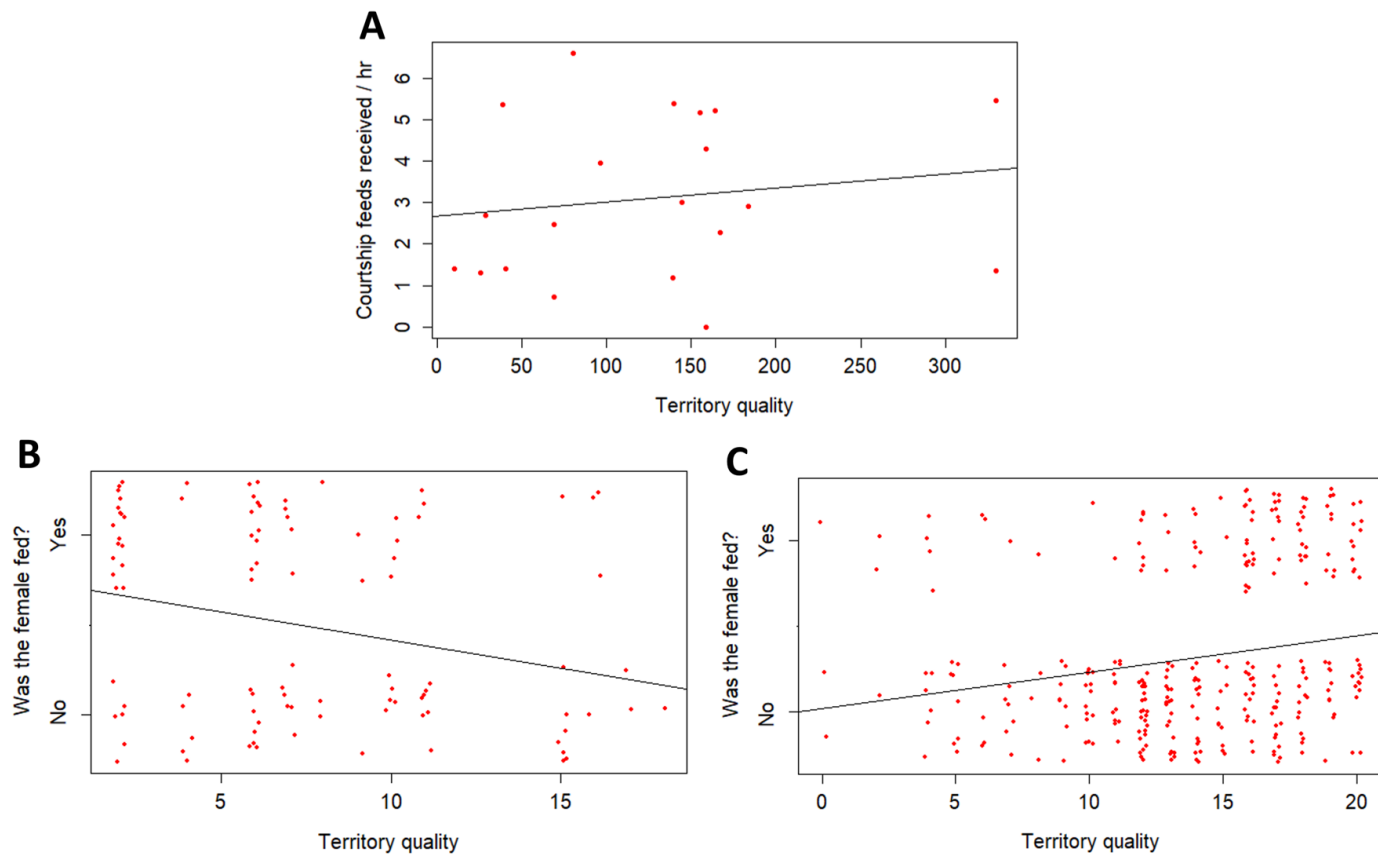


Figure 11: The impact of territory quality on courtship feeding. Courtship feeding increases with increasing territory quality in the focal observations in 2020 (Figure 11A) and in the extracted data 2016 – 2020 (Figure 11C), and decreases with increasing territory quality in the extracted data 2006 – 2009 (Figure 11B). Individual datapoints are shown in red, and are scattered around the values of 'Yes' and 'No' on the y-axis for easier visibility in Figures 11B and 11C. Lines of best fit are added in black. Note: territory quality is calculated in a slightly different way in the focal observations in 2020 and in the data extracted from the long-term database, resulting in different scales. A direct comparison between 11A and 11B&C is therefore not possible, 11B and 11C however are comparable.

5. DISCUSSION

In this project I addressed two different research questions concerning courtship feeding in the cooperatively breeding species *M. coronatus coronatus*. The first research question explores how cooperative breeding affects courtship feeding – is there load-lightening for the dominant male (Hypothesis 1a), or increased cumulative investment in terms of courtship feeding for the dominant female (Hypothesis 1b), and why do subordinates participate in courtship feeding (Hypotheses 1c&d)? The second research question investigates what role courtship feeding plays - that of paternal investment (Hypothesis 2a) or that of mating effort (Hypothesis 2b)?

Research question 1

Hypothesis 1b was unsupported in *M. coronatus coronatus* as there was no significant increase in courtship feeding levels with a greater number of subordinates in the group, in any of the datasets. The dominant female thus does not benefit from an increased number of subordinates via cumulatively increased levels of courtship feeding. The dominant male showed reduced courtship feeding effort in the presence of subordinates, which is consistent with load-lightening in the presence of subordinates, supporting hypothesis 1a. This mirrors the results of previous papers showing that other traits, such as maternal investment in eggs, are more likely to respond to

cooperative breeding through load-lightening rather than increased investment (reviewed in Dixit et al. 2017).

However, hypothesis 1a does not necessarily explain the fact that in two of the datasets (data from the years 2006 – 2009 and the breeding season 2020), the dominant female received significantly fewer courtship feeds in the presence of more subordinates: hypothesis 1a predicts that the increased feeds via the subordinates and the decreased feeds via the dominant male should cancel each other out, and therefore there should be no effect of number of subordinates on number of courtship feeds.

The cause underlying this reduction in total courtship feeds in the presence of subordinates is at this point unclear. One possibility is that this reduction is a maladaptive side-effect of group living: in larger groups, the dominant male may engage in more aggressive interactions with subordinates, shortening the time available for courtship feeding. However, this explanation is unlikely, as aggressive interactions are rare in *M. coronatus coronatus* (Teunissen et al. 2018), and thus should not represent a heavy opportunity cost even in large groups. A more promising explanation is that in the presence of subordinates, the dominant male reduces his courtship feeding effort further than what is compensated for by the subordinates: adaptive undercompensation. This would represent a surprising and novel result: theoretical papers (Johnstone 2011), backed by empirical findings (Hatchwell 1999, Koenig & Walters 2012) predict that in general, in cooperatively breeding species the reduction of investment from the dominants should be less than the increase in subordinate effort. However, a similar phenomenon, adaptive incomplete compensation, where one parent only partially compensates for a reduction in investment by the other, has been shown to be widespread and of great importance in bi-parental care, where it acts to ensure cooperation by ensuring that it is maladaptive for either party to leave parental investment to the other (Houston & Davies 1985; McNamara et al. 1999, Harrison et al. 2009). This raises the question whether the here observed undercompensation could fulfil a similar function to the incomplete compensation in bi-parental care. This hypothesis would rely on either side (dominant male or subordinate) being able to adjust their courtship feeding effort plastically to the other side's behaviour, and on undercompensation by the dominant male increasing cooperation from helpers – something that future studies may be able to elucidate. In general, exploring what selection pressures and mechanisms may have given rise to this surprising and, in the literature on cooperative breeding uncommon, observation of undercompensation may prove a fruitful avenue for future research.

Additionally, the question arises why subordinates help with courtship feeding in the first place. The data here showed a striking pattern: in the combined extracted dataset, only subordinates related to the dominant male fed the dominant female. This is in accordance with hypothesis 1d, which suggests that subordinates feed the dominant female to assist the dominant male in assuring his paternity. If courtship feeding done by subordinates represents alloparental investment in offspring (hypothesis 1c), then related subordinates and unrelated subordinates would both be expected to engage in courtship feeding: the former due to kin-selection, and the latter as they are more likely than related subordinates to inherit the dominant male's breeding position upon his death, at which point they benefit from group augmentation through successfully raised offspring (Kingma et al. 2011a). However, this does not exhaust the possible explanations for the observed pattern: whilst previous reviews have grouped the function of courtship feeding done by the sexual partner into two categories (paternal investment vs mating effort), I suggest that the same cannot be done as easily for courtship feeding done by a subordinate group member – indeed, a large body of literature (amongst others Reyer 1986, Richardson et al. 2002, Kutsukake & Clutton-Brock 2006, Radford & Du Plessis 2006, Kutsukake & Clutton-Brock 2010) has been dedicated to exploring the broad range of

functions of behavioural interactions between subordinates and dominants. Courtship feeding by subordinates may thus, for example, act to signal quality to a potential prospective mate or to strengthen social bonds to the dominant female, similar to other affiliative interactions (Teunissen et al. 2018). Overall, this study can therefore only represent a first foray into understanding why subordinate individuals feed the dominant female and a more detailed study will be necessary to unravel the drivers behind this behaviour. It will be especially worthwhile to analyze how relatedness to the dominant female, not only dominant male, impacts courtship feeding by subordinates.

Research question 2

In the second research question, I investigated several variables to determine whether courtship feeding functions as paternal investment or as mating effort. Courtship feeding has no impact on the reproductive output of the breeding attempt in question: none of the four measures of reproductive output, in neither of the three datasets, was significantly affected by courtship feeding. Similarly, courtship feeding also did not influence access to mating, measured via copulation rate. There is thus no direct evidence that courtship feeding takes the role of either parental investment or mating effort, as it affects neither reproductive output nor access to mating. Courtship feeding is observed with greater frequency before nest building starts (consistent with courtship feeding being an incentive for reproduction) and there is a nearly significant trend for its incidence to be predicted by the intensity of physical mate-guarding. This points indirectly to mating effort as function of courtship feeding. The results concerning territory quality are more difficult to interpret, due to opposing trends in the different datasets (see below). In summary, there is no direct evidence supporting either hypothesis, and some indirect indication from the timing of courtship feeding that its function may be that of a mating effort. The conclusion that courtship feeding does not impact reproductive output in *M. coronatus coronatus* is also in accordance with previous papers, which found that variance in reproductive output could be attributed to group size (Kingma et al. 2010) and rainfall (Hidalgo Aranzamendi et al. 2019) rather than female condition per se – these factors may outweigh differences in reproductive output caused by underlying variation in female condition, potentially making courtship feeding as a means to increase reproductive output by improving female condition obsolete.

However, in interpreting the results concerning the role of courtship feeding, there are several caveats to keep in mind: firstly, despite the effort to measure a variety of variables, it is not clear whether these fully capture the relevant parameters. For example, copulation rate may not accurately reflect access to reproduction: as shown in previous studies, the generally low copulation rates in *M. coronatus coronatus* indicate that this species does not use frequent copulations to assure paternity (Hall & Peters 2009). Instead, the incidence of extra-pair copulations (unfortunately difficult to measure; N. Teunissen, pers. comm.) might be a better measure of the resulting degree of paternity. Furthermore, several other processes may be acting which are difficult to account for: for example, it is not yet well understood what governs investment into egg production or investment into food provisioning. Increased investment into offspring at the egg stage due to courtship feeding (as predicted by the paternal investment hypothesis) might be compensated by reduced investment into food provisioning at the nestling stage. Adjustments of later investments may thus conceal the effects of courtship feeding at earlier stages. A final caveat is that *M. coronatus coronatus* form long-term pair bonds, and divorce is relatively rare (Kingma et al. 2009). This makes it difficult to decipher the impact that the timing of courtship feeding has, as various long-term consequences as well as impacts on the pair-bond itself need to be considered. For example, it may not be necessary to time paternal investments such that they increase after the female indicates commitment to reproduction

by initiating nest building, if divorce is not a concern. Future studies may be able to fill in some of the various missing puzzle pieces described above.

In addition to the complications outlined above, which are specific to the study system, studying the role of courtship feeding presents one fundamental problem: the roles of mating effort and paternal investment can be intrinsically linked and thus difficult if not impossible to distinguish. For example, demonstrations of paternal investment can be attractive and used as a sexually selected signal indicating mate quality (Lotem et al. 1999), thus also acting to increase mating effort. Conversely, in order to increase the mating effort, nuptial gifts need to be attractive and valuable to the dominant female – they are thus likely to improve her condition and increase her (and, by proxy, the male's) reproductive output (Vahed 1998). Overall, this can blur the lines between courtship feeding as paternal investment and courtship feeding as mating effort – which raises the question how clear the distinction between them is in nature, and emphasizes that they are by no means mutually exclusive.

One variable, which presented some difficulties in interpretation, was territory quality: what explains the opposing trends in the years 2006 – 2009 (in which courtship feeding decreased with territory quality), and the years 2016 – 2020 (in which courtship feeding increased with territory quality)? Looking at the change in territory quality over the years may help to clarify the pattern: due to various conservation efforts, the study site changed considerably during the last two decades, and the *Pandanus* growth along Annie Creek improved markedly. This is reflected in overall higher territory quality scores in 2016 – 2020 compared with 2006 – 2009. This may resolve the apparent contradiction between the data sets: the dataset from 2006 – 2009 shows that courtship feeding decreases as territory quality increases from low quality to medium quality, and the dataset from 2016 to 2020 shows that courtship feeding increases as territory quality increases from medium quality to high quality. The relationship of courtship feeding and territory quality may therefore best be characterized by a v- or u-shaped curve – a pattern that is also visible in the combined data from 2006 – 2020 (see Figure 20). There are various factors which could give rise to such a u-shaped curve. For example, group members may indeed increase their efforts in courtship feeding in low quality territories (explaining the pattern observed in 2006 – 2009), but find more prey items in high quality territories despite their reduced effort due to greater prey abundance (explaining the pattern observed in 2016 – 2020). This is supported by previous studies considering the impact of habitat quality on food provisioning to offspring, which found both increased food provisioning effort in low quality territories (e.g. Kloskowski et al. 2017), as well as greater provisioning rates due to greater prey abundance in high quality territories (e.g. Gruebler et al. 2018). It is also worth noting that *Pandanus* growth, which is here taken as a proxy of territory quality and certainly plays a big role, may not be the only variable of interest. Other characteristics of territories, such as the presence or absence of various vines, may also influence territory quality but are not yet well understood.

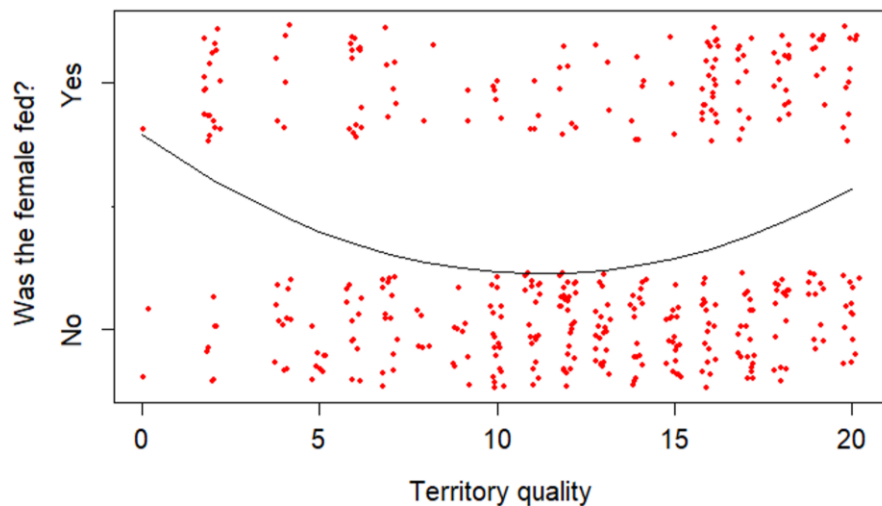


Figure 12: Presence or absence of courtship feeding during observations carried out in territories of differing quality, in the years 2006 – 2009 as well as in the years 2016 – 2020. The female is fed during fewer of those observations carried out in territories of intermediate quality, and during more of those observations carried out in territories of very low or very high quality. Individual datapoints are shown in red, and are scattered around the values of zero and one on the y-axis for easier visibility. A quadratic line of best fit is shown in black.

Consequences of data structure

The puzzle posed by territory quality discussed above is indicative of a general property of this project: it addresses the questions in three different datasets from nine different years. This structure or design of the data has various consequences and implications. It provides non-negligible benefits: the nine years cover a decade and a half, thus showing whether any trends in the data persist over time or are of transient nature, perhaps caused by unusual climatic conditions in one year. Using different datasets based on different methodologies can also control for artefacts emerging from particular aspects of data collection. On the other hand, the many differences in methodology can also cause several drawbacks which may be difficult to control for. One of these is the involvement of 16 different observers. Whilst I did control for observer identity by including it as a random effect in the models, the statistical analysis showed that there is a strong observer effect in several cases. Such observer effects are not uncommon in behavioural studies based on observations in the wild. The large number of observers in this study may compound the increase in noise due to observer effects, making it harder to detect statistically significant effects.

Another difficulty owed to the data structure is that in some cases, the conclusions from the different datasets contradict one another. This can, in some cases, be attributed to differences in methodology – for example, unlike in the other datasets, there is a high number of very short observations in the extracted data from 2016 - 2020, which are less likely to accurately reflect the courtship feeding level than longer observations. This might explain why the patterns relating courtship feeding to the number of subordinates cannot be seen in this dataset. However, disagreements between the datasets can also further illuminate the relationships between variables, as in the case of territory quality: here, the opposing trends observed in 2006 - 2009 and 2016 - 2020 may not be an artefact of differences in methodology but rather reflect the non-linear relationship between territory quality and rate of courtship feeding (as described above). Finally, some differences between the datasets may be attributed to environmental and climatic differences between the years. Tropical birds in general, and *M. coronatus coronatus* in particular, are sensitive to rainfall, as higher rainfall is associated with increased breeding success and invertebrate prey

abundance (Brawn et al. 2017, Hidalgo et al. 2019). Therefore, courtship feeding is likely of greater importance in drier years – which may explain some of the variation in results between datasets.

The data collected through focal observation in the breeding season 2020 is notable in this regard: unlike the other two datasets, which each encompass several years with varying climatic conditions, the focal observations reflect only a single wet season, which was uncharacteristically dry (Bureau of Meteorology, Australian government). Results based on this dataset are thus likely to show the importance of courtship feeding especially clearly. This makes it especially striking that even in the especially dry breeding season 2020, reproductive output was not affected by courtship feeding, further supporting the conclusion that courtship feeding does not act as paternal investment. Conversely, results based on the breeding season 2020 may not be applicable to behaviour in climatically more favourable, less dry years: dominant male courtship feeding effort, for example, was only assessed in the focal observations in 2020, and the observation of reduced dominant male effort in the presence of subordinates is consequently based on this dataset alone. However, the energy costs of obtaining food items for the dominant female are likely dependent on invertebrate abundance, which is lower in drier years (Brawn et al. 2017). The reduction in dominant male courtship feeding effort may hence be driven by the increased costs of courtship feeding in an especially dry breeding season, and may disappear under more regular climatic conditions.

Overall, this study provides a stepping stone for further investigation of the function of courtship feeding in *M. coronatus coronatus*, and calls for a more detailed analyses of this interesting behaviour.

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7. APPENDIX

The following tables show the output of the statistical models involved in this project. P values below 0.05 are shown in red, p values between 0.05 and 0.1 are shown in orange.

Model 1: What impacts courtship feeding in the focal observations in 2020?

Response variable: courtship feeding rate; linear model

Explanatory variable	Estimate	p value	t value	SE
Nr. Subordinates	-2.171454	0.0674	-1.972	1.101275
Nest stage	-0.973110	0.3344	-0.997	0.975765
Territory quality	0.013444	0.0488	2.144	0.006271
Date	0.025601	0.5379	0.630	0.040612

Model 2: Does courtship feeding impact nest abandonment in the focal observations in 2020?

Response variable: nest abandonment (Yes/No); generalized linear model

Explanatory variable	Estimate	p value	z value	SE
Courtship feeding rate	-0.10941	0.7590	-0.307	0.35665
Nest stage	-2.83736	0.0469	-1.988	1.42758
Date	-0.05427	0.3847	-0.869	0.06243

Model 3: Does courtship feeding impact the delay between completing the nest and laying the first egg in the focal observations in 2020?

Response variable: Delay between completing the nest and laying the first egg in days; linear model

Explanatory variable	Estimate	p value	t value	SE
Courtship feeding rate	-0.34690	0.5100	-0.675	0.51398
Nest stage	-4.67224	0.0416	-2.229	2.09656
Date	-0.12285	0.2017	-1.335	0.09201

Model 4: Does courtship feeding impact the willingness of the dominant female to copulate in the focal observations in 2020?

Response variable: Female interest in copulation per hour (Copulations + solicited but unsuccessful copulations per hour); linear model

Explanatory variable	Estimate	p value	t value	SE
Courtship feeding rate	-0.247408	0.220	-1.294	0.191250
Nest stage (Complete frame without lining : complete frame with lining)	0.080255	0.929	0.091	0.884995

Nest stage (Complete frame without lining : early frame)	0.512727	0.766	0.305	1.683691
Nest stage (Complete frame without lining : mid frame)	0.471061	0.656	0.457	1.029884
Date	0.009256	0.839	0.208	0.044571

Model 5: Does the dominant male courtship feeding effort change in the presence of subordinates in the focal observations in 2020?

Response variable: Male courtship feeding effort rate; linear model

Explanatory variable	Estimate	p value	t value	SE
Nr. subordinates	-2.610297	0.0425	-2.205	1.184061
Territory quality	0.005296	0.4205	0.827	0.006405
Date	0.044313	0.3195	1.027	0.043129

Model 6: What impacts courtship feeding in 2006 – 2009?

Response variable: Was the female fed during the observation (Yes/No);
generalized linear model with mixed effects

Explanatory variable	Estimate	p value	z value	SE
Mate-guarding intensity	0.5138	0.06479	1.847	0.2782
Nr. subordinates	-0.6688	0.03870	-2.067	0.3235
Territory Quality	-0.9690	0.00436	-2.851	0.3399
Observation length	0.4306	0.09552	1.667	0.2583
Season (Wet/Dry)	-0.1845	0.77654	-0.284	0.6499
Observer	-1.9460	0.10187	-1.636	1.1896

Model 7: Does courtship feeding affect nest abandonment in 2006 – 2009?

Response variable: nest abandonment; generalized linear model with mixed effects

Explanatory variable	Estimate	p value	z value	SE
Was the female fed?	-0.82985	0.350	-0.934	0.88881
Nr days during observation	-0.30431	0.825	-0.222	1.37248
Observation length	0.49042	0.766	0.297	1.65095
Observer	0.51813	0.572	0.566	0.91583
Season (Wet/Dry)	-0.08681	0.927	-0.092	0.94761

Model 8: Does courtship feeding affect clutch size in 2006 – 2009?

Response variable: Clutch size; linear model with mixed effects

Explanatory variable	Estimate	p value	t value	SE
Was the female fed?	0.03619	0.9213	0.100	0.36175
Nr days during observation	0.11185	0.8570	0.182	0.61293
Observation length	0.12989	0.8585	0.181	0.71929
Observer	-0.22579	0.6520	-0.458	0.49316
Season (Wet/Dry)	1.11121	0.0229	2.465	0.45076

Model 9: What impacts courtship feeding in 2016 – 2020?

Response variable: Was the female fed during the observation (Yes/No); generalized linear model with mixed effects

Explanatory variable	Estimate	p value	z value	SE
Nr. subordinates	-0.07058	0.650057	-0.454	0.15558
Territory Quality	0.48947	0.001934	3.100	0.15789
Nest stage (Before nest building: early stage)	-2.04621	0.000542	-3.459	0.59155
Nest stage (Before nest building: late stage)	-1.60557	0.012160	-2.507	0.64031
Nest stage (Before nest building: unknown stage)	-1.90175	0.001231	-3.232	0.58848
Observation length	0.43535	0.005432	2.780	0.15659
Continuous observation (Yes/No)	-0.36835	0.372342	-0.892	0.41290
Time of day (am/pm)	-0.52925	0.408090	-0.827	0.63976

Model 10: Does courtship feeding affect nest abandonment in 2016 – 2020?

Response variable: nest abandonment (Yes/No); generalized linear model with mixed effects

Explanatory variable	Estimate	p value	z value	SE
Was the female fed?	0.231398	0.5572	0.587	0.394204

Nr days during observation	0.059293	0.9338	0.083	0.713575
Observation length	0.003968	0.9837	0.020	0.194212
Nest stage (Before nest building: early stage)	-0.372729	0.7000	-0.385	0.967455
Nest stage (Before nest building: late stage)	-1.911451	0.0579	-1.896	1.008039
Nest stage (Before nest building: unknown stage)	-0.560787	0.6148	-0.503	1.114260

Model 11: Does courtship feeding affect clutch size in 2016 – 2020?

Response variable: clutch size; linear model with mixed effects

Explanatory variable	Estimate	p value	t value	SE
Was the female fed?	-0.194592	0.136	-1.505	0.129268
Nr days during observation	0.094833	0.652	0.453	0.209576
Observation length	0.007083	0.909	0.114	0.061947

Model 12: Does courtship feeding affect the number of live fledglings in 2016 – 2020?

Response variable: clutch size; linear model with mixed effects

Explanatory variable	Estimate	p value	t value	SE
Was the female fed?	-0.2757	0.51842	-0.651	0.4234
Nr days during observation	-0.9483	0.14838	-1.474	0.6434
Observation length	0.1693	0.39710	0.856	0.1978

Model 13: Does relatedness to the dominant male influence whether a subordinate feeds the dominant female in 2006 – 2009 and 2016 – 2020?

Response variable: Did the subordinate feed the dominant female (Yes/No);

generalized linear model with mixed effects

Explanatory variable	Estimate	p value	z value	SE
Is the subordinate	12.0921	< 0.001	5.551	2.1785

related to the dominant male (Y/N)				
Observation length	0.5133	0.0616	1.869	0.2746