

Offspring provisioning effort in European starlings (*Sturnus vulgaris*) during the  
nestling rearing period

by

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Abstract

Rearing offspring is a critical but energetically costly period for birds. Socially monogamous species typically have biparental care, although females invest more heavily in the offspring. Some studies have found that in the socially monogamous yet facultatively polygynous European starling (*Sturnus vulgaris*), females provisioned the offspring at similar rates as the males, with provisioning rates higher in the mornings than the afternoons. One study also found that provisioning rates tended to increase mid-way through the nestling cycle before declining. This study was conducted to confirm whether the findings in the literature also pertain to our European starling population. Parental provisioning by eight European starling pairs was studied over the nestling period using GoPro cameras. Two observation sessions (morning, afternoon) per pair were done on five different days through the nestling period. I predicted that male and females would provision offspring at a similar rate. I also predicted that offspring provisioning rates would be higher in the mornings than afternoons. Finally, I predicted that as nestlings aged, provisioning visits would increase. Females provisioned offspring significantly more often than males. Moreover, parents provisioned at higher rates in the mornings than afternoons. Finally, as nestlings aged, provisioning rates continued to increase. This study has implications in further understanding avian investment in offspring provisioning behaviours.

April 26, 2021

## Table of contents

<b>I. INTRODUCTION</b> .....	<b>3</b>
I.I Parental investment theory .....	3
I.II Risk and challenges in feeding behaviours of bird species .....	4
I.III Background information on European starlings .....	7
I.IV Feeding behaviours of European starlings .....	8
I.V Objective and question of this study .....	8
I.VI Predictions .....	9
<b>II. METHODS</b> .....	<b>10</b>
II.I Fieldwork .....	12
II.II Data collection .....	13
II.III Data analysis .....	15
II.IV Statistical analysis .....	16
<b>III. RESULTS</b> .....	<b>17</b>
III.I Differences between male and female provisioning rates .....	17
III.II Feeding rates affected by time of day and temperature .....	18
III.III Number of offspring provisioning visits per hour .....	19
<b>IV. DISCUSSION</b> .....	<b>20</b>
IV.I Parental provisioning differences .....	20
IV.II Provisioning efforts during optimum time of day and ambient temperatures .....	22
IV.III Rate of provisioning visits as nestling age .....	24
<b>ACKNOWLEDGEMENTS</b> .....	<b>28</b>
<b>REFERENCES</b> .....	<b>29</b>
<b>SUPPLEMENTAL INFORMATION</b> .....	<b>36</b>

## I: Introduction

### I.I Parental investment theory

Parental investment can be defined as the amount of work a parent puts toward their young to increase the young's chance of survival and future reproductive success (Trivers, 1972). Some of these investments seen in passerine species include but are not limited to incubation, feeding, teaching, and protecting offspring (Trivers, 1972). Therefore, offspring rearing is a critical period for birds (Kessel, 1957; Trivers, 1972), and offspring provisioning is one of the greatest investments made by parents. However, parental contributions between males and females can differ; in many species it is demonstrated that female contributions exceed that of their male counterparts (Trivers, 1972). To what extent males invest in parental care is one of the main issues in understanding sexual selection and mating systems (Sandell et al., 1996). Across avian species, male care is widespread and species-specific (Sandell et al., 1996). In European starlings (*Sturnus vulgaris*), a large portion of males breed monogamously; therefore, they exhibit biparental care where both parents contribute to rearing the young at similar rates (Sandell et al., 1996). Furthermore, Smith et al. (1994) state that biparental care is important in birds with altricial young (undeveloped nestling at the time of hatch), for increased growth and enhanced survival of the offspring. However, in facultatively polygynous relationships, where a male may have more than one female partner, there tends to be a decline in male parental contribution (Sandell et al., 1996). Moreover, as males engage in alternative activities, such as extra-pair copulations (EPCs) their rates of provisioning can be negatively affected (e.g., Komdeur et al., 2002; Sandell et al., 1996; Trivers, 1972).

Provisioning of offspring is done throughout the entire day (Grundel, 1987); however, parents allocate the majority of their feeding during certain times and temperatures as food abundance is most available during these periods (Kessel, 1957; Trivers, 1972; Verner, 1965). Kessel (1957) found that the most active hours for European starlings are during the mornings, late afternoons and early evenings.

The energy expended by the parent correlates positively with the number of nestlings they support. If there are many nestlings the parent needs to exert more energy to gather as much food as possible (Grundel, 1987). Additionally, the age of the nestling is positively correlated with an increase in energy expenditure by parents to maintain the feeding threshold of the growing nestlings (Kessel, 1957; Steen et al., 2012). Interestingly, Kessel (1957) specified from other published studies (e.g., Kluijver, 1933; Wallgraff, 1953) that in European starling populations, offspring provisioning rates initially increased; however, during Day 7 a plateau effect was noticed and continued until Day 17 and finally declined every day until fledging. It is believed that parents reduce their provisioning rates to their offspring towards the end of the nestling period to coax the grown nestlings to leave the nest (Steen et al., 2012).

### I.II Risk and challenges in feeding behaviours of bird species

Birds have adapted many skills through natural selection to gain access to quality food sources (Caraco, 1981). However, feeding in the wild comes with risks and challenges. The foremost challenge relates to food abundance, which can differ among various feeding grounds. Therefore, birds need to consider the amount of food in their environment for survival (Dunnet, 1955). In certain species of birds, such as European starlings, the supply of food can be the determining factor for the success in laying a

second clutch within a season (Dunnet, 1955). Additionally, Geiser et al. (2008) found that the abundance of food can determine a population's survival in a particular environment. If food availability is enough for each individual then there is a higher chance of nestling survival and if not, nestling mortality increases (Barras et al., 2021; Geiser et al., 2008; Rauter et al., 2002).

A subsequent challenge to consider during offspring provisioning is to ensure that no unnecessary energy is spent. During foraging, adult birds should avoid risky situations when they have satisfied their energetic requirements for their given body mass (Caraco, 1981; Lima, 1986). However, if the bird has exceeded its energy expenditure, then they would act in a risk-prone manner in return for a larger net benefit of food sources (Caraco, 1981). Barras et al. (2021) studied the daily activities of Alpine ring ouzel (*Turdus torquatos alpestris*) to better understand how they allocated their time and energy during specific periods of the day. It was understood that foraging for food was most preferred in early mornings depending on what type of food they ate and due to cooler temperatures (Barras et al., 2021; Rauter et al., 2002). This finding was supported by Biebach (1984) who found a negative correlation between energy expenditure and ambient temperature in incubating European starlings, indicating that the birds were expending more energy during cooler temperatures.

Another common challenge seen in most avian species is the issue of balancing the benefits of sustenance and the risk of predation. Natural selection favours the act of successful foraging with a decreased risk of predation (Bonter et al., 2013). Foraging behaviours are affected by the anticipated risk of predation; therefore, foraging sites are chosen by birds based on the minimum risk of predation and the efficiency of foraging (Bonter et al., 2013).

One final challenge seen in procuring food is experienced by altricial nestlings through competition with their siblings. Asynchronous hatching in many altricial bird species results in a size hierarchy amongst siblings (Bryant & Tatner, 1990; Nilsson & Svensson, 1996). The later hatched sibling is frequently the smallest and will be at a competitive disadvantage compared to their larger siblings (Nilsson & Svensson, 1996). When parents come with a single food item, the larger and stronger nestling typically receives it (Erickson, 2010; Kessel, 1957). This size hierarchy can result in decreased survival of the smaller, weaker nestling when food is limited (Erickson, 2010). Moreover, Kessel (1957) describes that offspring feeding frequencies increase in larger broods. Thus, it can be assumed that parents increase their energy expense to maintain sufficient levels of food provisioning in the brood (e.g., Steen et al., 2012). The energy spent by females laying eggs and by parents feeding their offspring is compromised when nestlings aggressively compete to maximize their food intake (Erickson, 2010). A study conducted by Stouffer and Power (1990) showed that asynchronous hatching increased nestling mortality in European starlings when sibling numbers were increased.

Consequently, parental energy expenditure is greatest for larger brood sizes and increases as nestlings age (Grundel, 1987). Grundel (1987) found that male Mountain chickadees (*Parus gambeli*) increased their provisioning rates in larger broods when compared to smaller broods, and when nestlings got older. Additionally, European starlings increased their rate of offspring provisioning as their brood size increased to meet the minimum food requirements of the total number of nestlings (Stouffer & Power, 1990). Support for increased rates in parental provisionings in larger broods has also been shown in Marsh tits (*Parus palustris* L.; Nilsson & Svensson, 1996), Black-throated blue warblers (*Dendroica caerulescens*; O'Neil-Goodbred & Holmes, 1996), and in White-

bellied swiftlets (*Collocalia esculenta*; Bryant & Tatner, 1990). Additionally, a positive correlation was found between nestling growth rate and ambient temperature in Lapland longspur (*Calcarius lapponicus*); therefore, the rate of nestling growth was dependent on environmental conditions which had contributing impacts on food availability and parental provisioning (e.g., Perez et al., 2016).

### I.III Background information on European starlings

In summary, adult birds face many barriers when obtaining food as they need to consider many risks and challenges for their own survival and that of their nestlings. European starlings are considered to be one of the most successful species to colonize new areas. They originated in Europe and parts of Asia and were introduced to North America in the 1800s (Cornell Lab of Ornithology, 2019; Feare, 1984). They are cavity-nesting ground-foragers (Kessel, 1957), inhabiting natural holes of trees, cracks and crevices of buildings and nest boxes if available (Cornell Lab of Ornithology, 2019). They are socially monogamous yet facultatively polygynous (Pinxten et al., 1993). They exhibit biparental care (Trivers, 1972), where both parents incubate the eggs for 12 days (Feare, 1984), and provision the offspring for the duration of the nestling period which lasts for 21-23 days (Komdeur et al., 2002; Sandell et al., 1996). They produce up to two broods per year, with an early brood in April and a late brood in June (Kessel, 1957). Females lay an average of three to six eggs per clutch (Cornell Lab of Ornithology, 2019). The altricial young depend heavily on their parents for food throughout the offspring rearing period (Kessel, 1957; Ricklefs & Peters, 1981).



#### I.IV Feeding behaviours of European starlings

Many avian feeding behaviours are species-specific (Dunnet, 1955). European starlings, the focal species of this study, tend to forage in open areas (mainly pastures), with other species such as Rock doves (*Columba livia*), American crows (*Corvus brachyrhynchos*), and American robins (*Turdus migratorius*) (Cornell Lab of Ornithology, 2019). Starlings are omnivorous and use their long, sharp beaks to probe the soil for insects, berries, and seeds (Feare, 1984; Linz et al., 2007). Moreover, according to Dunnet (1955), approximately 95% of their food during the breeding season is found underground. Most adult starlings introduce animal matters such as beetles, grasshoppers, crickets, and caterpillars into their diet earlier in the season as roosting populations start to increase (Dunnet, 1995; Fischl & Caccamise, 1987). Berries and seeds are later introduced into the diet as roosting populations exceed maximum size (Fischl & Caccamise, 1987). European starlings are also social feeders, but during the breeding season, parents pair up and visit certain feeding grounds together to collect food (Dunnet, 1955). Since the majority of the starling population exhibits a monogamous mating system, the male tends to invest in incubation and provisioning their nestlings as much as the female (Sandell et al., 1996). Thus, parents save energy due to both being involved in rearing their young. However, with larger brood sizes, the competition for food by nestlings increases. To counteract this, the parents tend to provision offspring more often (O'Neill-Goodbred & Holmes, 1996; Ricklefs, 2002).

#### I.V Objective and question of this study

The main objective of this study is to examine the parental investment of European starlings in food provisioning and to determine whether there are any changes in

provisioning over the nestling rearing period. The different factors included in this study were the sex of the provisioning parent (male versus female), the time of day (morning versus afternoon) with their associated ambient temperatures, and finally the age of the nestlings.

#### I.VI Predictions

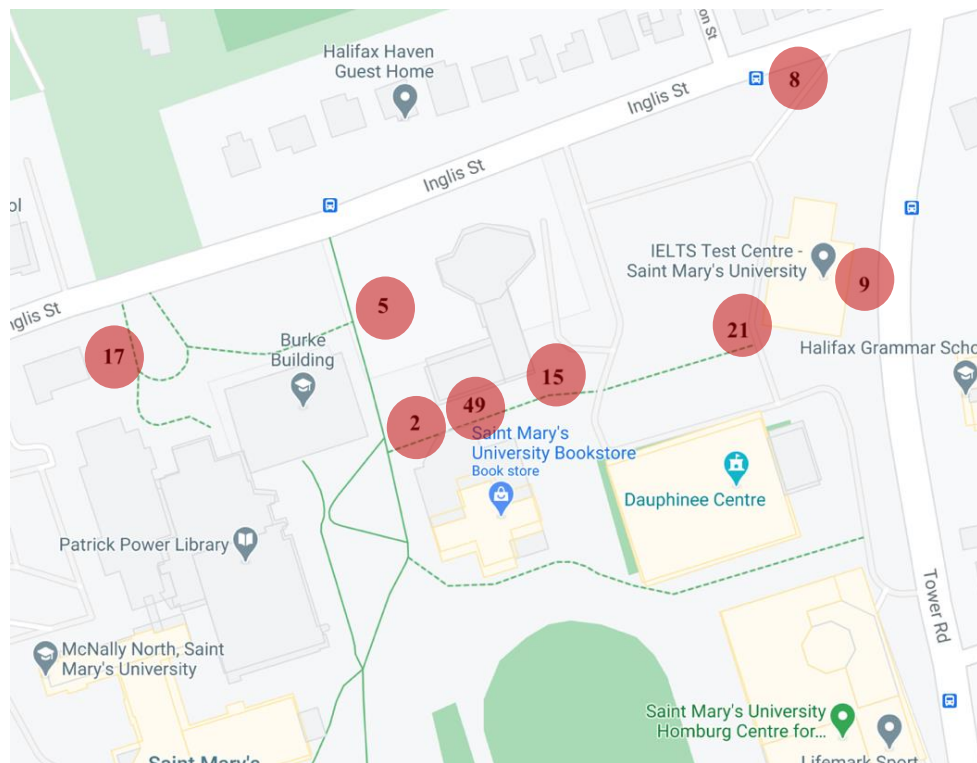
The first prediction of this study is that both male and female starlings will provision their offspring at similar rates. Since most starlings breed monogamously, socially mating with one female will allow the males to focus their attention and spend energy on one clutch/brood at one specific nest box rather than having to contribute to young in more than one nest box (Sandell et al., 1996). A study by Pinxten et al. (1993) found that in socially monogamous European starling pairs, both males and females provisioned at similar rates. My second prediction is that cooler summer temperatures (mornings) will result in more foraging activities. Furthermore, parents will provision their offspring more frequently in the mornings compared to the afternoons, due to invertebrates being closer to the surface of the soil. A study conducted by Rauter et al. (2002) on Water pipits (*Anthus spinoletta*) demonstrated that as ambient temperatures increased, parents decreased their offspring provisioning rates. The survival and activities of the ground invertebrates preferred by Water pipits were temperature sensitive. The final prediction is that the number of provisioning visits will increase with the age of nestlings since a nestling's energy requirements increase as they develop. As demonstrated in Kessel's (1957) study, European starlings showed an increase in provisioning visits as nestlings matured in age.

This research aims to fill in the gap of understanding parental investment in feeding behaviours of European starlings. It will further increase our knowledge about this species and their behaviours with respect to offspring provisioning. Starlings are widespread in Nova Scotia, but their population sizes here and in their native range are declining (The Cornell Lab of Ornithology, 2019). Therefore, studying their offspring provisioning behaviours can be applied to broader conservation efforts in Canada and elsewhere. This study can contribute to understanding whether nestlings are not receiving sufficient amounts of food, resulting in a decline in species numbers. If we can better understand the offspring provisioning behaviours of European starlings, we can apply this knowledge to other avian species that are endangered or near extinction.

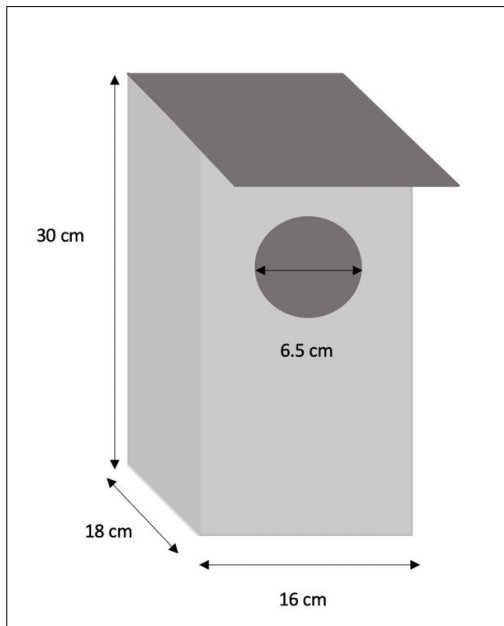
## II: Methods

The research was conducted on the Saint Mary's University campus, located in Halifax, Nova Scotia, Canada ( $44^{\circ} 37' 32.43''$  N  $-63^{\circ} 34' 28.25''$  W) (Figure 1). The research start date was June 15<sup>th</sup> and ended on July 12<sup>th</sup>, 2020, encompassing the late (second) breeding period for European starlings. The early (first) breeding period was missed due to the global Covid-19 pandemic. There are a total of 42 nest boxes spread around campus. The dimensions of the boxes are consistent for each of the 42 nest boxes in length, width, and depth respectively, measuring 30cm x 16cm x 18cm. Additionally, a roof was made for the nest boxes with privacy hooks on the sides to fasten the roof to the top of the box. The entrance hole was centered in the middle of the front side of the nest box and was 6.5cm in diameter (Figure 2). The boxes were screwed onto tree trunks and were approximately 1.5 to 2.5 meters (150 to 250 cm) from the ground.

Only 14 of these 42 nest boxes were occupied by breeding adults for the late brood. Many females already had eggs in their nest when this study began. Five clutches were not successful (the eggs did not hatch) due to predation on adults. During the 2020 breeding season, there was high predation activity by raccoons; they were seen on top of the nest boxes with remnants of the dead adult(s) found near the nest boxes. Furthermore, one of the clutches had already hatched before the study began; therefore, nest box 42 was disqualified. This study focused on the remaining eight nest boxes, as the eggs in these nest boxes hatched within the given incubation period. The nests were located in the area bound by Inglis Street and Tower Road and had the following numbers: 2, 5, 8, 9, 15, 17, 21 and 49 (Figure 1).



**Figure 1:** Map of Saint Mary's University campus located in Halifax, NS Canada. The red circles signify the location of eight nest boxes along Inglis Street and Tower Road.



**Figure 2:** Front view design and measurements of a drawn nest box available throughout Saint Mary's University campus.

### II.I Fieldwork

Nests were monitored daily throughout the laying period until two days after the last egg was laid. At this stage, the parents were incubating their eggs, giving us a rough estimate of when hatching would occur. Kessel (1957) stated that starlings generally begin their incubation period after the last or the penultimate (second to last) egg is laid. Therefore, the date of expected hatch is typically 12 days from the time that the final egg has been laid (Kessel, 1957), with hatching periods lasting one to two days (Stouffer & Power, 1990).

The nests were checked again two days prior to hatching and on the expected hatch date until all eggs had hatched. Intensive monitoring occurred throughout the rearing period to document nestling mortality. The nestling rearing period typically lasts between 21 to 23 days before the nestlings fledge (Dunnet, 1955). During this three-week period, the nests were checked to keep track of the number of nestlings. Clutch sizes

varied from three to six eggs (n=8 clutches) while brood sizes ranged from one to five nestlings (n=8 broods).

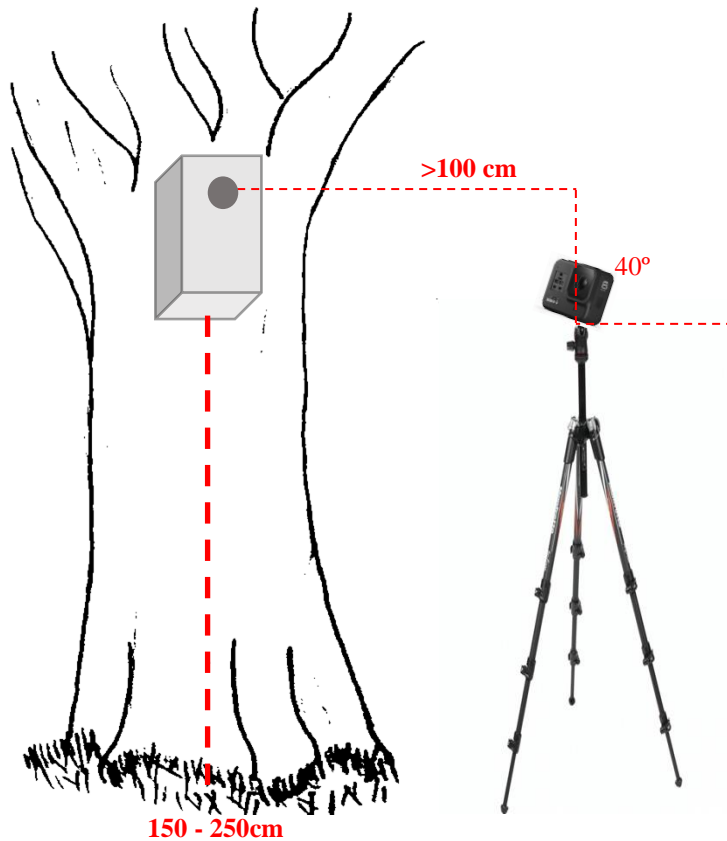
On Days 5 and 11 (Day 0 is considered the day of the first hatch), nestlings were checked by Dr. Barber to ensure that feeding was continuing by observing the developmental progress of the offspring. Additionally, adults were captured inside their nest boxes and banded when nestlings were between five and fifteen days old. Two types of bands were used, one on each tarsus. Males were given a yellow-coloured plastic band on their right tarsus above an aluminum Canadian Wildlife Service (CWS) band, indicating that they were males. Females were given a pink coloured plastic band on their right tarsus above their CWS band. Furthermore, the birds received two coloured plastic bands of a unique combination on their left tarsus so that we could distinguish each adult from the others. These bands allowed me to identify the sex of the parent when they went inside their nest box to provision their offspring. The banding was conducted by Dr. Barber and Maheshi Dharmasiri (M.Sc. student).

## II.II Data collection

The first offspring-provisioning watch was conducted on Day 3 after the nestlings were hatched, with June 18<sup>th</sup>, 2020 being the first such watch. GoPro HERO8 cameras were set up immediately prior to each watch using a tripod to hold the camera in place. The tripods were prepared before the watches by wrapping green tape around the legs. Additionally, artificial tree branches were randomly wrapped onto the tripod legs for camouflage (Figure 3). Recordings were done on Days 3, 7, 13, 17, and 20 of the nestling rearing period. These days were randomly chosen to best track and observe nestling development within the 21 to 23 day rearing period. Several watches (n=5) were re-recorded the

following day if the parents did not provision their offspring when the camera was set up during one of the initial recording days. On Day 7 for specific nest boxes (n=2), an artificial tree was placed between the legs of the tripod to further blend the camera into the surroundings. This was because I had noticed that there was a stop in the feeding activities of the adults on Day 3, likely due to the camera being placed beside their nest box. Therefore, the use of an artificial tree helped hide the camera to allow parents to resume normal offspring provisioning. This method worked well for Nest Box 5 and so the process was continued for all sequential watches for this nest. It did not help with the other nest box that was also experiencing abnormal feeding rates (Nest Box 9); therefore, manual watches were conducted on Nest Box 9 from Day 13 and onwards.

The cameras were placed on the right side of each tree trunk with the side of the nest box visible for recording. This method allowed the camera to clearly record the bands on the right tarsus (the sex-identifying bands) of the birds going into the nest box. There was a minimum total distance of 100 centimeters from the cavity of the nest box to the camera. The cameras were angled approximately 40° to have a direct and clear view of the nest box hole, as shown in Figure 3.



**Figure 3:** The observational setup of the GoPro Hero 8 camera in relation to the nest box.

The batteries of the cameras lasted between 1.17 to 1.33 hrs of recordings per nest box. At the start of each watch, the date, time and nest box number were recorded. Furthermore, the Environment Canada webpage for Halifax was used to determine the temperature in Celsius ( $^{\circ}\text{C}$ ) for that particular time of day. The recordings were conducted twice a day per nest box. In the mornings, recordings were done between 0700 h and 1000 h. The afternoon recordings were done between 1300 h and 1730 h.

### II.III Data analysis

During video analysis, only one hour of the video for each nest box was observed, starting when a parent first went inside the nest box to feed the offspring. Few of the



watches (n=12 out of the 80 watches) did not start feeding within 10 to 20 minutes of recording, resulting in them having less than one hour of observed recording time. Therefore, recordings length ranged from 25 minutes to one hour within eight nest boxes. Moreover, out of the 80 videos recorded during the rearing period, eight videos were omitted as they had less than 54 minutes of recording. It was decided by Dr. Barber that this amount of time would be sufficient per watch. Therefore, the observational time ranged between 54 minutes to one hour. Only 72 watches were within these time ranges.

Using the Topaz Sharpen AI v2.2.0 software (Addison, Texas, United States of America) to help clarify the sex of the parent if it was unclear. On every occasion that the parent went inside the nest to feed, a screenshot was taken and transferred into Topaz to edit for pixilation so as to achieve a clear image of the bird's head. This method was only used during the earlier nestling period when the parents were not banded. European starlings can be sexed by the colour of their beak. Females tend to have pale pink colouration on their lower mandible, whereas the males have a bluish coloured lower mandible (Kessel, 1951). During the later nestling period, when all of the parents were banded, the sex of the parent was identifiable by looking at their band colours on the right tarsus (yellow vs. pink).

#### II.IV Statistical analysis

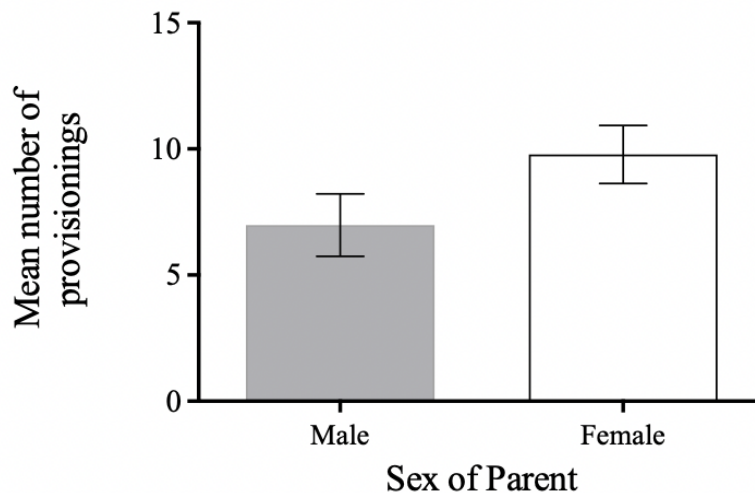
To test for normality of all data, d'Agostino-Pearson normality test was conducted. A paired t-test was used to determine if offspring provisioning rates differed between male and female adult starlings. A paired t-test was also used to compare the number of offspring provisioning visits between mornings and afternoons as well as to compare ambient temperature between morning and afternoon watches. A repeated measure test

(Friedman test) was done to determine if the total number of provisioning visits (by both parents) changed as nestlings get older over the five days sampled over the nestling period. Results were considered significant when  $P < 0.05$ .

### III: Results

#### III.I Differences between male and female provisioning rates

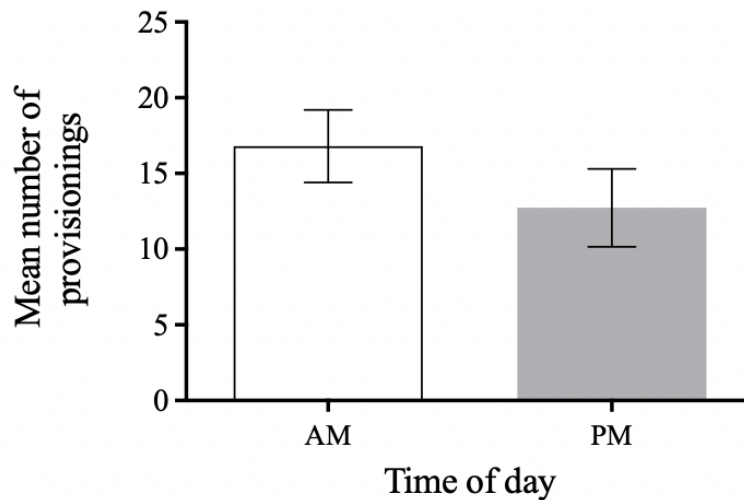
As predicted, there was a significant difference in the rate of offspring provisioning between males and females (paired  $t = 2.98$ ,  $df = 7$ ,  $P < 0.02$ ; Figure 4). On average, females fed at a significantly higher rate (mean number of provisionings/ hour + SE:  $9.76 \pm 1.15$ ) than did males ( $6.98 \pm 1.24$ ) over the nestling rearing period. The total average number of offspring provisioning (across all eight broods) made by females was  $78.28 \pm 1.15$ , whereas males had a total average of  $55.82 \pm 1.24$  ( $n = 8$  broods).



**Figure 4:** Bar graph demonstrating the average number of offspring provisioning visits  $\pm$  SE per hour made by the male and female parent at eight different broods ( $n = 8$ ).

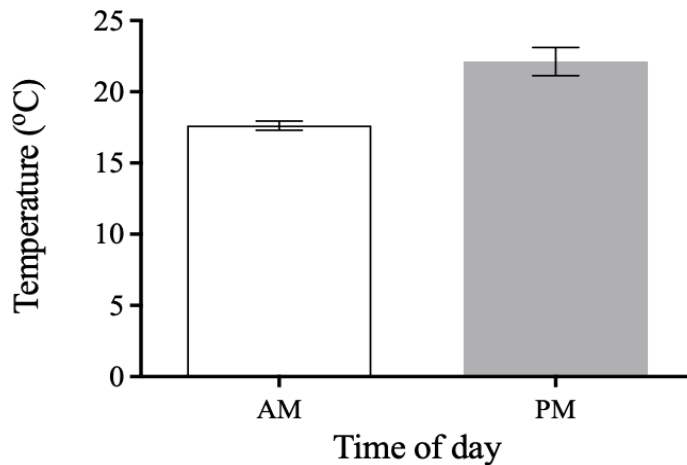
### III.II Feeding rates affected by time of day and temperature

Offspring provisioning rates were significantly higher in the mornings than in the afternoons (paired  $t= 2.52$ ,  $df= 7$ ,  $P < 0.04$ ; Figure 5). The average number of provisioning per hour  $\pm$  SE was  $16.80 \pm 2.40$  in the mornings compared to  $12.73 \pm 2.57$  in the afternoons.



**Figure 5:** Bar graph representing the average number of provisioning visits  $\pm$  SE per hour between the morning and afternoon observation periods ( $n= 8$  broods).

Ambient mean temperature was significantly higher in the afternoons than in the mornings over the June to July (2020) study period (paired  $t= 3.81$ ,  $df= 7$ ,  $P<0.007$ ; Figure 6). The average temperature in the mornings  $\pm$  SE was  $17.63 \text{ }^\circ\text{C} \pm 0.32$ , compared with the average afternoon temperatures of  $22.13 \text{ }^\circ\text{C} \pm 0.99$ .

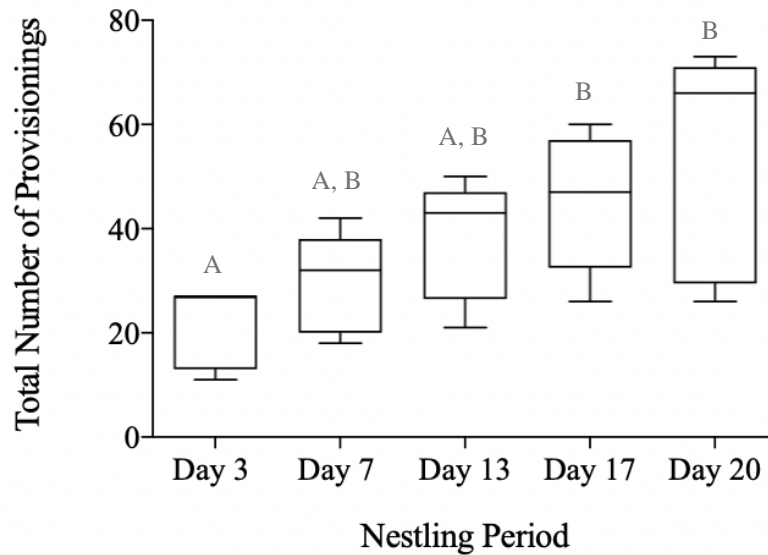


**Figure 6:** Bar graph representing the average ambient temperature  $\pm$  SE in the mornings compared to afternoons in June and July 2020.

### III.III Number of offspring provisioning visits per hour

The number of offspring provisioning visits per hour by both parents increased significantly over the nestling period ( $F_T = 15.47$ ,  $df = 4$ ,  $P < 0.004$ ; Figure 7). The significant differences were found between Day 3 and Day 17, and between Day 3 and Day 20, with parents provisioning Day 3 nestlings at a significantly reduced rate than they did when nestlings were 17 and 20 days old.

The least variance in provisioning visits occurred on Day 3, with an average percent time of provisioning ranging from 11.72% to 31.08%. Furthermore, the most variance occurred on Day 20, with an average percent time of provisioning ranging from 25.96% to 80.84%.



**Figure 7:** Box plots of the mean total number of offspring provisioning over five different days of the nestling period ( $n=5$  broods). Box plots with an alphabetical letter over them are significantly different from those with a different letter over them.

#### IV. Discussion

##### IV.I Parental provisioning differences

Passerine species have altricial young so food provisioning by the parents is critical for the successful growth and development of the offspring (Steen et al., 2012). One of the major findings in this study was that female European starlings provisioned offspring at significantly higher rates than did males over the rearing period (from Day 3 until Day 20). Many studies on European starlings have found that females provision offspring at higher rates than males (e.g., Kessel, 1957; Komdeur et al., 2002; Pinxten et al., 1993; Sandell et al., 1996; however, see Pinxten et al., 1993; Sandell et al., 1996). Trivers (1972) stated that females have the greatest initial contribution to parental investment as they fertilize and house the egg for development before laying, which commits the female to continuing to invest heavily in their development. However, males may help in one or

more aspects of parental care, such as constructing the nest, incubating the eggs, protecting and feeding the offspring (Trivers, 1972). A male's earlier investment is considered to be initially less than that of the female's, perhaps resulting in males reducing their parental investment during the rearing period (Trivers, 1972). Furthermore, the concept of male parental care due to the confidence of paternity plays a large role in brood contribution by males. Whittingham et al. (1992) highlighted that in male avian species as paternity certainty increase, so too did their level of provisioning the offspring with food. Additionally, Komdeur et al. (2002) discussed that males may engage in alternative activities to seek the attention of other mates for extra-pair copulations (EPCs), thereby reducing their provisioning efforts (Kessel, 1957; Trivers, 1972).

Two studies on European starlings found that there were fewer offspring provisionings by polygynous males as males divided their workload amongst another nest, whereas males in a socially monogamous relationship provisioned offspring at similar rates as females (Pinxten et al., 1993; Sandell et al., 1996). However, studies such as those by Filliater and Breitwisch (1997) on Northern cardinals (*Cardinalis cardinalis*) and by Grundel (1987) on Mountain chickadees found that males had higher offspring provisioning rates than females. Bart and Tornes' (1989) study on House wrens (*Troglodytes aedon*) suggested that when males contribute substantially during the raising of the offspring, it not only increases the survival of the offspring, but also keeps the female in good condition to lay eggs for the second clutch, or to have her mate with him again in the following season.

#### IV.II Provisioning efforts during optimum times of day and ambient temperatures

Supplying food to nestlings is not only important for growth but also for their increased survival (e.g., Rauter et al., 2000). In altricial species, when parents provision at lower rates it can affect brood survival, especially during cooler ambient temperatures when food demands are at their highest to produce energy (Rauter et al., 2002). Therefore, for adults to successfully provision their offspring, they must provision in higher rates during optimum times of the day and at optimum ambient temperatures (Verner, 1965). In this study, it was found that the mornings were the most preferred time for European starlings to provision their offspring as compared to the afternoons. Morning summer temperatures were significantly cooler than those in the afternoons. Thus, findings of this study support that in the mornings, when temperatures were cooler, offspring provisioning rates were highest in European starlings compared to afternoons.

A study conducted by Barras et al. (2021) on Alpine ring ouzel demonstrated that during the feeding of offspring, parents most efficiently foraged during rainfalls and cooler ambient temperatures, as it increased the availability of earthworms that account for the bulk of the nestlings' diet (Barras et al., 2021).

The activities and survival of arthropods are dependent on ambient temperature (Rauter et al., 2002). Therefore, the increase in food supply might be due to the most preferred temperature and weather conditions of the arthropods (Rauter et al., 2002). Furthermore, Rauter et al.'s (2002) study on Water pipits showed that during higher temperatures, females decreased their offspring feeding rates. As a result, the most active parental response to food demands of nestlings was shown to occur during cooler temperatures (Rauter et al., 2002). Additionally, Barras et al. (2021) found that during lower temperatures, parental provisioning visits increased to manage the increased energy

expenditure by the thermoregulating nestlings. However, Verner's (1965) study on Long-billed Marsh wrens (*Telmatodytes palustris*), another grounder feeder, demonstrated that there was an increase in offspring provisioning rates in higher ambient temperatures due to higher visibility, activity, and availability of insects on the surface of the wet marshes. Moreover, Geiser et al. (2008) described a positive correlation between offspring feeding frequency and ambient temperature. They found that the ground-dwelling ants, the most preferred diet of Wryneck (*Jynx torquilla*) were most accessible when they were on the surface of the soil, which occurs only during certain temperatures. However, if the temperatures were too cold or too warm, then the ants would burrow deep into the soil, becoming inaccessible (Geiser et al., 2008).

Hence, studies have demonstrated that ambient temperatures play a key role in arthropod accessibility, leading to a positive correlation in avian foraging activities (Geiser et al., 2008; Rauter et al., 2002). Ground-feeding passerine species with an insectivorous diet forage during certain temperatures, when their preferred diet is most abundant on the surface of the soil (e.g., Barras et al., 2021; Geiser et al., 2008; Rauter et al., 2002; Verner, 1965). Thus, the optimal time of day and temperature to provision offspring at an increased rate depends on the specific avian species. This study suggests that arthropods were most available during the earlier times of the day, when temperatures were cooler, compared to afternoons, as this was noted to be the most active provisioning period in this population of European starlings, between these two time periods.



#### IV.III Rate of provisioning visits as nestling age

Provisioning visits increased significantly over the nestling period of European starlings between Day 3 and Day 17 and between Day 3 and Day 20. This finding is likely due to the growing nestlings having increased energetic demands. In European starlings, Kessel (1957) found that the number of provisioning visits started to stabilize between Day 7 and Day 15 with Days 17 and 18 showing a steady decline each day. A study on Black-throated blue warblers showed that as nestlings aged, provisioning rates and the biomass of food increased (O'Neill-Goodbred & Holmes, 1996). The same patterns were seen in other passerine species (e.g., Barba et al., 2009; Grundel, 1987; Morehouse and Brewer 1986; Steen et al., 2012), with one exception being the Nashville warbler (*Vermivora ruficapilla*) (Knapton, 1984). In the warbler species, there was no change in provisioning rates during the nestling period, with food loads remaining stable as nestlings aged (Knapton, 1984).

The quantity of food delivered can affect the survival of nestlings by evidence of partial or complete brood reduction (O'Neill- Goodbred & Holmes, 1996). More food can be provided through bigger load sizes or more frequent parental provisioning visits. This study only focused on provisioning rates. Older nestlings need more food compared to when they are younger (e.g., O'Neill- Goodbred & Holmes 1996; Steen et al., 2012). As their growth rates increase, they require more energy (Steen et al., 2012). Furthermore, when Water pipit nestlings were approximately 6 to 8 days old, parents started to increase feeding rates in response to their nestlings' pressure for more food by their loud begging behaviours (Rauter et al., 2000). The demands for food were the highest when the brood sizes were larger or when temperatures were cooler (Rauter et al., 2000).

In general, parental provisioning increases with nestling age, especially during the stage when the offspring growth rate is at its peak (Steen et al., 2012). Kessel (1957) found that starling nestling growth rates were highest towards the end of the second week (Days 11-12), and when the nestling is close to their final body mass, the number of provisioning visits tends to level off and start to decline (Barba et al., 2009; Kessel, 1957; Grundel, 1987; Steen et al., 2012). Additionally, in many passerine species, including European starlings prey load size also tends to increase as the swallowing capacity of the nestlings develop as they age (Slagsvold & Wiebe, 2007; Kessel, 1957). However, prey load size was not examined in this study.

A study conducted by Steen et al. (2012) on Eurasian kestrels (*Falco tinnunculus*) showed that the maximum daily rate of prey mass was 100.5 g<sup>-day</sup> which was on Day 16, compared to 71.7 g<sup>-day</sup> during Day 9 of the rearing period. Moreover, when the kestrels neared their time of fledging (Day 28-32), the food load was dropped to 47-56 g<sup>-day</sup> (Steen et al., 2012). This pattern of rising and plateauing phases of parental provisioning was seen in Great tits (*Parus major*; Gibbs, 1950), Black-throated blue warblers (O'Neill-Goodbred & Holmes, 1996), House sparrows (*Passer domesticus*; Seel, 1969), and European starlings (Kessel, 1957; Tinbergen, 1981); however, my population of European starlings lacked this pattern. I only observed parental provisioning behaviour until Day 20 of the nestling period whereas nestlings fledge between 21 and 23 days of age (Sandell et al., 1996). It is possible that provisioning rates levelled off closer to fledging as suggested by other studies (e.g., Blondel et al., 1991; Grundel, 1987). Moreover, Kluijver (1933) and Wallgraff's (1953) work on European starlings found a decline in offspring provisioning visits starting on Days 17 and 18. It is interesting that the local European starling population that I studied had a continuation of increasing

provisioning visits until Day 20. Therefore, there may be a likelihood that food abundance and ambient temperatures allowed this population to continue to increase their offspring provisioning rates. Further studies should be conducted to look at environmental factors and the abundance of food that may affect fledging periods, resulting in fewer or more provisioning visits from parents in European starlings.

To conclude, the results of this study showed that female starlings fed at higher rates than males. This may be due to lower paternity confidence although females may have reduced maternity confidence due to intraspecific brood parasitism (Lynch et al., 2019). It could also be due to males engaging in alternative activities (Trivers, 1972). Passerine species provision their offspring throughout the entire day; however, adults had higher rates at certain times of the day and at certain ambient temperatures. European starlings showed a significantly higher rate of provisioning during the mornings when summer temperatures were cooler than those of the afternoons. These findings suggest that food availability was highest during the mornings. Alternatively, parents could have more energy in the mornings after a night of rest. Finally, provisioning visits increased significantly towards the end of the nestling period (Days 17 and 20) compared to the start (Day 3). Therefore, as nestlings aged, they demanded a higher food supply to fulfill their energetic costs as their growth rates increased.

The European starling populations in both North America and in their native ranges are declining. Future studies can continue to explore parental investment behaviours regarding feeding by looking at additional factors (brood size, weather, food abundance, quantity of food, predatory risks, etc.) to determine whether parental investment behaviours change over time and whether it causes negative effects such as reduced fledging success. Analyzing these factors with respect to offspring provisioning

behaviours can allow us to better understand the practices and contribution of parental investment, as it greatly impacts the chances of offspring survival and future reproductive success. This study allows for a more in-depth understanding of European starlings and the parental provisioning efforts that they exhibit. Hopefully this study will lead the way into the development of more research opportunities on this passerine species. The new information learned on the starling populations can then be applied to other avian species who may be at the risk of endangerment which can initiate conservation efforts.

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## Supplemental information

**Table 1:** The average number of provisioning visits  $\pm$  SE by parents for eight broods.

Nest box Number	Male	Female
15	11.1	12.7
9	3.6	5.71
49	10.44	12.1
17	6.56	6.38
21	9.56	11.6
5	1	6.33
2	7.89	9.56
8	5.67	13.9

	Male	Female	Paired t test	
Number of values	8	8	Table Analyzed	Males vs Females
Minimum	1	5.71	P value	0.0206
25% Percentile	4.118	6.343	Significantly different? (P < 0.05)	Yes
Median	7.225	10.58	One- or two-tailed P value?	Two-tailed
75% Percentile	10.22	12.55	t, df	t=2.976 df=7
Maximum	11.1	13.9	Number of pairs	8
Mean	6.978	9.785	Correlation coefficient (r)	0.6898
Std. Deviation	3.495	3.257	P value (one tailed)	0.0292
Std. Error of Mean	1.236	1.152	Was the pairing significantly effective?	Yes
Lower 95% CI of mean	4.056	7.062		
Upper 95% CI of mean	9.899	12.51		
Sum	55.82	78.28		

**Table 2:** The average number  $\pm$  SE of provisioning visits in the mornings and afternoons by parents for all eight broods.

Nest box number	Morning	Afternoon
15	28.2	19.4
9	12.75	3.67
49	20.6	22.4
17	10.8	11.2
21	18.4	11.2
5	6.33	2
2	16.75	18
8	20.6	14

	Morning	Afternoon
Number of values	8	8
<b>Minimum</b>	6.33	2
25% Percentile	11.29	5.553
Median	17.58	12.6
75% Percentile	20.6	19.05
<b>Maximum</b>	28.2	22.4
<b>Mean</b>	16.8	12.73
Std. Deviation	6.797	7.263
<b>Std. Error of Mean</b>	2.403	2.568
Lower 95% CI of mean	11.12	6.662
Upper 95% CI of mean	22.49	18.81
<b>Sum</b>	<b>134.4</b>	<b>101.9</b>

Paired t test	
Table Analyzed	Provisioning morning vs afternoon
P value	0.04
Significantly different? (P < 0.05)	Yes
One- or two-tailed P value?	Two-tailed
t, df	t=2.517 df=7
Number of pairs	8
Correlation coefficient (r)	0.7903
P value (one tailed)	0.0098
Was the pairing significantly effective?	Yes

**Table 3:** The average temperatures  $\pm$  SE in the mornings versus the afternoons over all offspring provisioning visit recordings at each nest box.

Nest Box numbers	Morning temperatures (°C)	Afternoon temperature (°C)
15	16	23
9	18	24
49	18	20
17	18	19
21	18	26
5	17	24
2	19	18
8	17	23

	Morning temperatures (°C)	Afternoon temperature (°C)
Number of values	8	8
Minimum	16	18
25% Percentile	17	19.25
Median	18	23
75% Percentile	18	24
Maximum	19	26
Mean	17.63	22.13
Std. Deviation	0.9161	2.8
Std. Error of Mean	0.3239	0.9899
Lower 95% CI of mean	16.86	19.78
Upper 95% CI of mean	18.39	24.47
Sum	141	177

Paired t test	
Table Analyzed	Temperature morning vs. afternoon
P value	0.0066
Significantly different? (P < 0.05)	Yes
One- or two-tailed P value?	Two-tailed
t, df	t=3.813 df=7
Number of pairs	8
Correlation coefficient (r)	-0.4804
P value (one tailed)	0.1141
P value summary	ns
Was the pairing significantly effective?	No

**Table 4:** The total number of provision visits by both parents for five nest boxes over the five observation days of the nestling period.

Nest box Number	Day 3	Day 7	Day 13	Day 17	Day 20
15	27	34	50	54	73
49	27	32	43	47	66
17	15	22	21	26	26
21	11	18	44	60	69
8	27	42	32	39	33

**Table 5A:** Supplemental information for **Table 4** (Figure 7).

	Day 3	Day 7	Day 13	Day 17	Day 20
Number of values	5	5	5	5	5
Minimum	11	18	21	26	26
25% Percentile	13	20	26.5	32.5	29.5
Median	27	32	43	47	66
75% Percentile	27	38	47	57	71
Maximum	27	42	50	60	73
Mean	21.4	29.6	38	45.2	53.4
Std. Deviation	7.797	9.633	11.51	13.29	22.1
Std. Error of Mean	3.487	4.308	5.148	5.945	9.882
Lower 95% CI of mean	11.72	17.64	23.71	28.69	25.96
Upper 95% CI of mean	31.08	41.56	52.29	61.71	80.84
Sum	107	148	190	226	267



**Table 5B:** Supplemental information for **Table 4** (Figure 7).

Number of families	1			
Number of comparisons per family	10			
Alpha	0.05			
Dunn's multiple comparisons test	Rank sum diff.	Significant?	Summary	
Day 3 vs. Day 7	-9	No	ns	A-B
Day 3 vs. Day 13	-8	No	ns	A-C
Day 3 vs. Day 17	-15.5	Yes	*	A-D
Day 3 vs. Day 20	-17.5	Yes	**	A-E
Day 7 vs. Day 13	1	No	ns	B-C
Day 7 vs. Day 17	-6.5	No	ns	B-D
Day 7 vs. Day 20	-8.5	No	ns	B-E
Day 13 vs. Day 17	-7.5	No	ns	C-D
Day 13 vs. Day 20	-9.5	No	ns	C-E
Day 17 vs. Day 20	-2	No	ns	D-E
Test details	Rank sum 1	Rank sum 2	Rank sum diff.	
Day 3 vs. Day 7	5	14	-9	
Day 3 vs. Day 13	5	13	-8	
Day 3 vs. Day 17	5	20.5	-15.5	
Day 3 vs. Day 20	5	22.5	-17.5	
Day 7 vs. Day 13	14	13	1	
Day 7 vs. Day 17	14	20.5	-6.5	
Day 7 vs. Day 20	14	22.5	-8.5	
Day 13 vs. Day 17	13	20.5	-7.5	
Day 13 vs. Day 20	13	22.5	-9.5	
Day 17 vs. Day 20	20.5	22.5	-2	