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The Nutritional Value of Fecal Sacs: Testing the Parental Nutrition Hypothesis

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THE NUTRITIONAL VALUE OF FECAL SACS: TESTING THE PARENTAL NUTRITION HYPOTHESIS

by

AMANDA W. BURNS

(Under the Direction of C. Ray Chandler)

ABSTRACT

Nest sanitation is an important aspect of parental investment in birds with altricial nestlings. Passerine nestlings produce fecal matter that is encased in a mucous membrane for easy disposal. These fecal sacs are either removed from the nest and transported a distance away or they are ingested by the adult. A decline in fecal sac ingestion rates as nestlings age has been observed in several species. The parental nutrition hypothesis posits that this pattern can be attributed to increasing digestive efficiency as nestlings age. The parental nutrition hypothesis makes three predictions: fecal sac consumption rates should decrease as nestlings age, the nutritional value of fecal sacs should decline as nestlings age, and females should consume more fecal sacs than males. I tested these predictions in Eastern Bluebirds (*Sialia sialis*) using video cameras in order to quantify changes in behavior over the nestling cycle and analysis of protein content of fecal sacs. Both male and female bluebirds consumed fecal sacs significantly less often as nestlings aged. Protein content ($\mu\text{g/g}$) of fecal sacs also declined with age. Female bluebirds consumed more fecal sacs than males. Overall, my results support the parental nutrition hypothesis, although multiple selective factors may affect consumption of fecal sacs.

INDEX WORDS: Fecal sac, Coprophagy, Nest sanitation, Altricial nestlings, Parental nutrition hypothesis, Eastern Bluebird

THE NUTRITIONAL VALUE OF FECAL SACS:
TESTING THE PARENTAL NUTRITION HYPOTHESIS

by

AMANDA W. BURNS

B.S., Rochester Institute of Technology, 2011

A Thesis Submitted to the Graduate Faculty of Georgia Southern University in

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MASTER OF SCIENCE

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DEDICATION

I dedicate this to my beloved parents, Anne and Dana. Their unconditional love and support, as well as their seemingly infinite patience and strength, provide an invaluable foundation in my life.

Almost 13 years ago they faced the possibility of losing their 15 year-old daughter after I suffered a stroke and had emergency open heart surgery. The stroke left no significant or noticeable physical damage, but left a lasting emotional impression on our family. My parents watched over me closely as I recovered. Without the devotion, wisdom, and love they each showered me with in the challenging weeks, months, and years that followed, I may never have completed my Bachelor's degree, let alone a Master's degree thesis.

Years later, after investing three years of study in my undergraduate major (American Sign Language Interpreting), I made the difficult decision to change my major to align with my newfound love of birds. Again, my parents were each there for me with unyielding love and support.

A single dedication page is insufficient space to express the gratitude, admiration, and love I have for the two amazing individuals responsible for my genetic code. But to you, Mom and Dad, who have gone above and beyond with your parental investment, I dedicate this research.

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INTRODUCTION

One of the most demanding phases of any animal's life is reproduction, particularly the rearing of offspring. While some animals do not invest time in parental care, leaving their offspring to fend for themselves, others invest substantial resources to the task at a cost to their own well-being. Parental investment is any expenditure of time and/or energy that increases an offspring's fitness at a cost to the parent, typically by decreasing the parent's ability to dedicate resources to other offspring (Trivers 1972). Parental investment can take many forms: resource provisioning, protection from predators, survival skill instruction (e.g., migration routes, hunting techniques), nest sanitation, etc. Ultimately, natural selection shapes variable patterns of parental investment in response to ecological and environmental pressures (Trivers 1972, Skutch 1976). For example, birds vary their post-hatching parental care as a function of the development stage of the young upon hatching.

Some birds (e.g., galliforms, charadriiforms) have nidifugous and precocial young, meaning that within 24-48 hours of hatching the young are active, forage independently, and partially regulate their body temperature. In contrast, passerine species have nidicolous and altricial young that are blind and helpless when they emerge from their eggs. For these reasons, altricial nestlings generally require greater post-hatching parental investment than precocial nestlings. Adults must collect food items and bring them to the nest site, brood the chicks (because they are initially incapable of maintaining their own body temperature), defend the nest from predators, and maintain a secure and sanitary environment for the chicks. The duties of parenthood present a resource management challenge that gives rise to a variety of strategies for balancing the time and energy requirements of the adult versus those of the offspring.

Nest sanitation is an important component of investment in altricial nestlings for several reasons. Minimizing the waste matter within and around the nest maintains warmth and dryness, and sanitation helps to deter infestations of pathogens or parasites (Skutch 1976, Lang et al. 2002). Parasites increase the cost of reproduction in birds (Møller 1993). Furthermore, the removal of fecal material from the nest reduces odors that may alert predators to the presence of the nest (Weatherhead 1984, Petit et al. 1989).

Many passerine nestlings (and the young of some other bird species; e.g., roadrunners, certain woodpeckers) have a mechanism that facilitates nest sanitation. After being fed a food item a nestling will often void a fecal sac (Skutch 1976, Welty and Baptista 1988). Therefore, an adult can deliver a food item to the nest and remove the conveniently packaged waste in a single visit. A fecal sac consists of fecal and urinary matter encased in a mucous membrane (Herrick 1900, Morton 1979, Weatherhead 1984). Adult passerines retrieve fecal sacs from the nest (and sometimes directly from the cloaca of a nestling) with their beaks (Skutch 1976). The mucous membrane surrounding the waste matter will break or split open on occasion (Herrick 1900), but typically stays intact while being handled by the adult.

In the event that a nestling does not void a fecal sac shortly after being fed, the parent will sometimes attempt to stimulate the nestling to produce a fecal sac. This behavior is most often referred to as “prodding” because a common form of stimulation is for the adult to use its beak to poke the cloaca of the nestling (or the area around it). The adult tugging on the down of the nestling is another reported stimulation behavior (Smith 1942, Skutch 1976). There are anecdotal reports in the literature of rather intense stimulation, such as Smith’s observation of a female Reed Bunting (*Emberiza*

schoenichus) that grabbed a nestling's head in her beak and shook it after less insistent methods of stimulation failed to produce a fecal sac. After having its head shaken, the nestling did void a fecal sac (Smith 1942).

Once an adult bird has retrieved a fecal sac, a decision regarding its disposal must be made because there are two methods of waste removal available to the adult. Fecal sacs can be removed from the nest and transported some distance away, or they can be ingested by the adult. Parent birds avoid the option of depositing fecal sacs on the ground below a nest or placing them on a convenient nearby branch because this attracts predators (Herrick 1900, Weatherhead 1984, Welty 1988, Petit et al. 1989, Lang et al. 2002). Thus, transport or consumption are the only viable options, and each has different potential costs and benefits.

Weatherhead (1984) summarized the costs of transporting a fecal sac away from the nest site. First, time and energy is spent in transport, especially if the adult is traveling in a direction different from the direction of its next foraging site. Travelling to a location solely for the purpose of fecal sac disposal has been observed in Common Grackles (Cliburn 1978). A second cost is the decrease in flight efficiency caused by the added weight and shifted center of gravity. Petit & Petit (1987) questioned Weatherhead's conclusion that the energetic and temporal costs of removing fecal sacs were significant. Petit et al. (1989) noted that there was likely some selective pressure for nest sanitation behavior, given the amount of effort the adults of many species put into it. Even when waste is transported away from the immediate vicinity of the nest, it may still pose some risk of alerting predators to the presence of a nest in the area. Tree Swallows (*Tachycineta bicolor*) minimize this risk by transporting fecal sacs long distances and

varying the direction from the nest where the fecal sac is deposited (Weatherhead 1984). Finally, there is a tradeoff cost. Transporting waste away from the nest requires time and energy that could otherwise be spent foraging or brooding. However, carrying the fecal sac away from the nest does avoid the introduction of parasites, pathogens, or un-nutritious waste into the digestive tracts of the adults (McKay et al. 2009) that would come with consuming a fecal sac.

Alternatively to transporting fecal sac, many species have been observed consuming the fecal sacs of their offspring (Blair and Tucker 1941, Tucker 1942). Of the 132 species and subspecies included in Tucker's (1941) review, 51 were noted to swallow the fecal matter of their nestlings at some point. Tucker's summary included both passerine and non-passerine species. Of the 15 orders represented, 4 included species that were observed swallowing the fecal matter of their offspring (20 families out of 45). Ingesting a fecal sac provides the same sanitation benefits as transport and eliminates the time and energy required to transport fecal sacs away from the nest. The cost of consumption is that it may have some detrimental effect on the digestive system of an adult because fecal sacs contain waste products of the digestive system (Hurd et al. 1991). If such a negative effect is real, it likely increases with the age of the nestlings because fecal sacs increase in size as nestlings age (Morton 1979, Weatherhead 1984, Hurd et al. 1991). Consuming fecal sacs could also introduce parasites into an adult's body (McKay et al. 2009). The widespread nature of fecal sac ingestion (at least 20 families in 4 orders) suggests that in some instances the benefits of ingestion outweigh the costs. It has even been suggested that the waste matter of the fledglings of some passerine species may have an "agreeable taste" (Skutch 1976).

HYPOTHESES

There are four principal hypotheses to explain patterns of transport/consumption of fecal sacs: the parental satiation hypothesis (McKay et al. 2009), the economic disposal hypothesis (Hurd et al. 1991), the nest predation hypothesis (Herrick 1900, Ibáñez-Álamo et al. 2013), and the parental nutrition hypothesis (Morton 1979, Glück 1988).

The parental satiation hypothesis (McKay et al. 2009) suggests that the consumption of fecal sacs by parent birds is a method of hunger suppression that allows them to continue provisioning nestlings at a high rate. In a study of fecal sac ingestion by Spotted Towhees (*Pipilo maculatus*), McKay et al. (2009) compared rates of fecal sac ingestion to male and female nest attendance and feeding rate. They found that fecal sac ingestion increased with brood size and that the parents of the heaviest nestlings ingested the smallest number of fecal sacs. Overall, this study sought to examine relationships between fecal sac ingestion and varying pressures on the breeding adults depending on food availability, brood size, and sex.

The economic disposal hypothesis (EDH) suggests that consuming the fecal sac is a better option than spending time and energy to transport it away from the nest, especially if other parental duties (i.e., brooding or foraging) are more pressing (Hurd et al. 1991, McGowan 1995, McKay et al. 2009). According to the economic disposal hypothesis the nutritional content of a fecal sac has no bearing on whether it will be consumed or not. The decrease in fecal sac consumption rates as nestlings age (Conder 1948, Glück 1988, Hurd et al. 1991, McGowan 1995, Lang et al. 2002) is the result of an increase in fecal sac size as nestlings age, and therefore a greater cost on the digestive

system of the adult from swallowing such fecal sacs. Hurd et al. (1991) do not specify how the content of a fecal sac would stress the digestive system of an adult passerine, but make this conclusion based on the logic that fecal sacs contain the digestive waste products of nestlings.

Herrick (1900) initially hinted at the nest predation hypothesis, but the idea was developed in greater detail by Ibáñez-Álamo et al. (2013). Because parental activity around a nest increases the probability of a predator locating the nest, it may be advantageous for parent birds to decrease the number of nest visits whenever possible. This could mean that an adult opts to swallow a fecal sac instead of making a trip to dispose of it. Ibáñez-Álamo et al. (2013) predict that the higher the nest predation risk, the higher the rate of fecal sac ingestion will be. This hypothesis also predicts that fecal sac ingestion rates in males and females will be roughly the same, in contrast to the parental nutrition hypothesis and economic disposal hypothesis, which both predict that the female will consume more fecal sacs than the male.

The parental nutrition hypothesis posits that fecal sacs have nutritional value because the digestive system of an altricial nestling has not finished developing, and nutrients are only being partially absorbed (McGowan 1995). This concept was proposed as far back as 1900 (Herrick 1900). As the nestlings age and their digestive efficiency increases, the nutritional content of their waste should decrease. If the nutritional value of fecal sacs decreases with nestling age, then adults have less to gain by ingesting the fecal sacs of older nestlings in comparison to the fecal sacs of younger nestlings. Because a parent bird is spending a significant amount of time and energy collecting food items for its nestlings, the fecal sacs present an opportunity to ingest nutrients and water, while

simultaneously maintaining nest sanitation. The parental nutrition hypothesis has also been referred to as the recycling hypothesis (Dell’Omo et al. 1998). Evidence supporting the parental nutrition hypothesis has been reported in at least three studies (Glück 1988, McGowan 1995, McKay et al. 2009).

The parental nutrition hypothesis has led to speculation about what resources (water, macro- or micronutrients) may be the primary driving force selecting for fecal sac consumption. For example, Greater Roadrunners (*Geococcyx californianus*) may benefit significantly from the water in fecal sacs (Calder 1968). The fecal sacs of Mountain White-crowned Sparrow nestlings (*Zonotrichia leucophrys oriantha*) were found to contain between 71.3 and 84.6 % water (Morton 1979). The calcium and protein content of fecal sacs is of special interest given that the female in particular may need to replace these nutrients after egg laying (McGowan, 1995). In multi-brooded species like the Eastern Bluebird (*Sialia sialis*) this potential energy source may be of even greater importance.

The parental nutrition hypothesis relies on the idea that nestling digestive efficiency improves post-hatching until it plateaus at a level comparable to that of an adult. The development of the digestive system of young birds has not been as widely studied in passerines as it has been in more economically valuable groups such as Galliformes. However, research has given some insight into the internal physiological and biochemical changes that may affect digestive efficiency. As nestlings age they grow in size both internally and externally. The increase in the size of digestive organs is not solely responsible for the increase in digestive efficiency in nestlings. Certain pancreatic and intestinal digestive enzymes in nestling House Sparrows (*Passer domesticus*)

increase through fledging (Caviedes-Vidal and Karasov 2001). In addition, Caviedes-Vidal and Karasov (2001) found that both pancreatic and intestinal protein content were significantly lower in hatchling House Sparrows than in older nestlings. Additional research of the physiological and biochemical development of the digestive system of altricial nestlings could provide further evidence in support of the parental nutrition hypothesis.

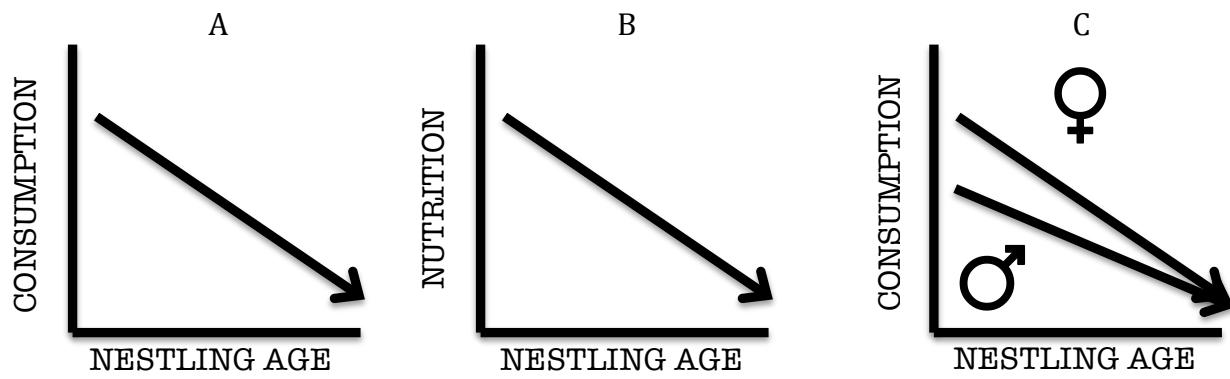


Figure 1. Parental nutrition hypothesis predictions tested in this study. First (left): Fecal sac consumption rates should decline as nestlings age. Second (middle): The nutritional content of fecal sacs should decline as nestlings age. Third (right): Females should consume more fecal sacs than males.

These four hypotheses make a number of predictions, many of them overlapping. Ultimately, however, the parental nutrition hypothesis makes a set of three predictions (Fig. 1) that together suggest that nutrition available in fecal sacs is an important driver of fecal sac consumption. First, adult birds are expected to consume fewer fecal sacs as nestlings age (Fig. 1A). This decline is precisely because the nutritional value of fecal sacs decreases (Fig. 1B). Finally, females should consume more fecal sacs than their male counterparts because of the higher initial investment of producing a clutch of eggs (Fig. 1C). The economic disposal hypothesis makes two similar predictions (Fig. 1A, 1C), but

in contrast to the parental nutrition hypothesis, it predicts that the decrease in fecal sac consumption is associated with an increase in fecal sac size as nestlings age, not a decrease in nutritional value.

The economic disposal hypothesis has been examined by several biologists in the field by analyzing the frequency of fecal sac removal over time and the placement of removed sacs outside of the nest (Weatherhead 1984, Petit and Petit 1987, Petit et al. 1989, Lang et al. 2002). Similarly, the parental nutrition hypothesis has been tested by making field observations of the occurrences of fecal sac consumption by a parent as the nestlings age (Dell’Omo et al. 1998). Some studies made observations of parental management of fecal sacs in order to test both hypotheses (McGowan 1995, McKay et al. 2009). Little has been done to examine the contents of fecal sacs in a laboratory setting, with the exceptions of Glück (1988), Hurd et al. (1991), and Morton (1979). Weatherhead did obtain fecal sacs from Tree Swallow nestlings and weigh them in the course of his study. Although Weatherhead’s results indicate an increase in the weight of fecal sacs from 1 to 13 days after hatching, his methods of analysis have been challenged.

OBJECTIVES

The objective of this study is to test three predictions from the parental nutrition hypothesis (Fig. 1). First, fecal sac consumption rates should decrease as nestlings age. Second, the nutritional value of fecal sacs is expected to decline as nestlings age. Finally, females should consume more fecal sacs than males.

To test these predictions, I quantified the behavior of male and female Eastern Bluebirds (*Sialia sialis*) via video recording of visits to the nest. I also collected fecal sac

samples from nestlings and had them analyzed for protein content. I chose to focus on the protein content of fecal sacs because of the important role protein plays in egg-laying in females (McGowan 1995).

METHODS

I made observations and collected fecal samples at 31 nestboxes between April 12 and August 7, 2014, at nine field sites across Bulloch County, Georgia (Table 1). Field sites were selected with Eastern Bluebird habitat preferences in mind (open spaces such as golf courses, meadows, and fields). The nestboxes were placed at least 50 m apart from one another at sites with multiple boxes.

Behavior of adult Eastern Bluebirds, including fecal sac consumption, was monitored by mounting small cameras on the tops of nestboxes. I purchased pre-built boxes made from Eastern Red Cedar from Lowe's and modified them to allow the placement of a small camera on the roof (Fig. 2). Internal dimensions of the nestbox were 10.5 x 10.25 x 18.3 cm. External dimensions of the boxes measured 12.5 x 13.6 x 32.5 cm. The entrance hole measured 3.8 cm in diameter. Any rough edges were smoothed by hand with sand paper to prevent splinters from harming the birds. Each box was modified with a hinge, a protective plastic food storage container, and a left-side window prior to being transported to a field site for placement. I mounted the bird boxes to 2.54-cm diameter metal conduit poles and placed them approximately 2.0 m from the ground. I attached each nestbox to the pole with U straps to hold the box to the pole and a picture-hanging hook to prevent the box from sliding down the length of the pole (Fig. 2).

Table 1. Location, number of nest boxes, and general description of study sites, Bulloch County, Georgia

Field Site Number	# of Boxes	Description	Latitude	Longitude
1	2	Residential development with few trees	32.3535361° N	-081.7587306° W
2	7	Undeveloped, managed land (mowing, prescribed burns)	32.6204139° N	-081.8786111° W
3	10	Agricultural/Residential	32.3115694° N	-081.7275139° W
4	1	Residential backyard adjacent to a golf course	32.3616611° N	-081.7777667° W
5	1	Residential front yard	32.4240694° N	-081.7685389° W
6	1	Residential backyard adjacent to a small corn field	32.4110944° N	-081.7180583° W
7	2	Residential property	32.3952111° N	-081.7844778° W
8	6	Undeveloped/Agricultural	32.6158444° N	-081.8780278° W
9	1	Residential backyard	32.4138333° N	-081.7670000° W



Figure 2. Three views of the modified nestbox.. Left: Back/side view showing the side window and the two U straps used to secure the box to the metal conduit pole. Middle: Forward view, showing the entrance and a camera mounted on the hinge inside the protective container. Right: View from above showing the camera rig through the protective plastic container

MODIFICATIONS TO NESTBOXES

I drilled one 32-mm diameter hole in the roof of each box to permit the camera to record events inside the nestbox, and one 32-mm diameter hole was drilled on the box's left side to increase the amount of light entering the box (Fig. 2). A 5-cm, zinc-plated strap hinge was mounted just above each roof hole, with one side screwed into the roof and the other side standing vertically so that the hinge created a ca. 70° angle. A Command™ Picture Hanging strip (medium size, 69.85 mm x 15.875 mm) was placed on the vertical hinge flap. Each camera was fitted with an additional Command™ strip, allowing the cameras to be efficiently placed and removed whenever needed.

The cameras were not waterproof, so I placed a protective shield on the roof of each nestbox in the form of a bottomless clear food storage container (Fig. 2). I used Loctite® clear silicone waterproof sealant to glue a container to each nestbox roof. I was able to easily access the cameras by unscrewing the container lid. The plastic container enclosed the entirety of the hole, the hinge, and the camera. The screw-off lid allowed access to the camera rig and protection from the elements. The food storage containers withstood 4 months of outdoor exposure before beginning to deteriorate. After roughly 5 months the plastic Tupperware had begun to thin and crack. The design worked well for my purposes, but modifications would have to be made for a nestbox to withstand multiple breeding seasons.

The cameras were not designed for low-level light conditions. When testing the camera system prior to the 2014 breeding season I determined that an insufficient amount of light was entering the nest boxes, even on a sunny day, for the camera to record bluebird activity inside the box. Thus, I drilled a hole into each nest box's left side,

roughly 13 cm above the bottom of the interior of the box. Optix® acrylic sheets (10.2-cm long by 6.5-cm high, 2.032-mm thick) were placed over the hole to prevent rain and wind from entering through it. The acrylic sheets were attached with Loctite® clear silicone waterproof sealant. A series of crossing lines were drawn over the “window” with green Sharpie™ to prevent the bluebirds from confusing the window with the true entrance/exit hole.

NESTBOX CHECK PROCEDURE

I checked nest boxes as often as possible, but no more than twice a day. Most boxes were checked every other day. After hatching, at each nest check I removed nestlings between the ages of 2-14 days and placed them in a temporary holding “nest” made from a Rubbermaid® 1.2 L food storage container and 100% cotton washcloth. With one exception, I did not handle or remove Day One hatchlings because of their small size. It was not unusual for nestlings to void a fecal sac after being placed in the temporary holding nest or even during transfer. When this happened, I transferred samples from the hand or the washcloth into a glass vial. If nestlings did not void a fecal sac as a result of being handled, I applied slight pressure to the abdomen (Morton 1979). In the event that neither handling nor light pressure on the abdomen produced a fecal sac, I fed the nestling a portion of a dried mealworm (Hurd et al. 1991).

I used non-toxic, washable Crafty Dab™ poster paint markers (yellow, red, green, and blue) to mark nestlings on the head and/or back in order to distinguish individuals within each brood. Paints and dyes are often used to color-mark birds (Calvo and Furness 1992). These markings were visible in the camera recordings. I marked birds younger than five or six days old on the back instead of the head because of the relative difficulty

of marking the head as well as the relative pressure it took to apply paint to the head as compared to the back. As the nestlings' feathers grew in, the paint began to disappear. I remarked nestlings every few days or as needed with the same color they were originally marked with. All procedures were approved by Georgia Southern University's Institutional Animal Care and Use Committee (protocol # I14008).

Occasionally minor repairs had to be made to the nest boxes during a nest check. Replacing a worn-out Command™ strip and adjusting the angle of a hinge using dental floss were the most common repairs needed. Other repairs included tightening screws and applying additional silicone around the base of the Tupperware camera shield. Command™ strips would begin to split and fall apart after a few weeks of use; the adhesive would lose integrity after prolonged exposure to heat and sun.

CAMERAS

I purchased 13 cameras, Camstick-HD DVRs, and used them to record activities within the nest boxes. I selected the cameras primarily for their small size (74.5 x 28 x 13 mm), relative low cost (\$72), and ability to record and store up to 8 GB of video and audio data without the need for external connections and wiring. The cameras recorded video in AVI format, 1280 x 720 at a maximum of 26 frames per second (fps). Audio data was recorded in WAV format: 176 Kbps. The cameras were capable of recording in motion-activated mode and sound-activation mode in addition to continuous recording mode. In motion-activated recording mode, the cameras switched from 26 fps recording to 1 fps recording after 10 seconds of inactivity. In sound-activated mode the cameras stopped recording after 3 seconds of low to no sound. I used motion-activated and continuous recording modes to monitor bluebird boxes, but not the sound-activated

recording mode. While testing the cameras prior to monitoring any nestlings, I discovered that wind can trigger recording when the camera is set to sound-activation mode. This made the other recording modes more practical.

The cameras were originally designed for use as home security devices, and so were not meant for exposure to extreme temperatures or rain. The food storage container protection system worked well to prevent rain from reaching the cameras and only one camera succumbed to the heat towards the end of the field season.

I charged cameras with a USB-to-wall-outlet cable. I placed fully-charged cameras in a nestbox and recorded until the memory card was full. I collected cameras the next time the box was visited, and I placed another camera in the box if one was available. I downloaded each camera's recordings to an external harddrive. I cleared the camera's memory and charged its battery so that it was ready for deployment in another nestbox.

VIDEO RECORDING

I used Quicktime to view video files. I reviewed 203 hours and 32 minutes of video. I played files back at either 4x or 3x normal speed until an adult bluebird arrived at the nestbox, a nestling showed signs of voiding a fecal sac, or another notable activity occurred, such as a nestling fledging. At that point the video was viewed at normal speed/real time. I viewed each nest visit by an adult bluebird no faster than real time; occasionally I viewed a nest visit either in whole or in part at less than 1x speed in order to discern the particulars of events. I did not view video any faster than 4x speed because the audio playback ceased at that point.

Using video recordings I quantified the frequency and length of nest visits, the frequency of feedings, method of nest sanitation (consume fecal sac or transport it), and the frequency of prodding.

I could easily distinguish the male from the female adult during nest visits from the onset of breeding season until mid-July. Around mid-July the males' breeding plumage became faded and it was more difficult to identify the sex of the adult bluebirds. When I did not know the hatch date, I determined nestling age using physical characteristics, fledging date, the date the clutch was completed, and the date the nestlings opened their eyes.

FECAL SAC ANALYSES

Sixty-one fecal sacs were analyzed for total protein content. The fecal sacs were collected from 18 different boxes (at least 36 individual nestlings in 23 different broods, 16 breeding pairs) between the hours of 0900 and 1915 hours (EST) over the course of the nestling period; mean time of collection was approximately 1500 hours.

I stored each fecal sac in a labeled glass vial, one sample per vial. I placed the samples on ice in a portable Coleman® cooler after collection until they could be placed in a freezer. Samples were kept frozen until I prepared them for shipping.

I sent the samples to the Proteomics and Mass Spectrometry facility, Donald Danforth Plant Science Center, St. Louis, Missouri. The samples were packaged with dry ice and sent overnight to make sure they did not thaw out before arrival. First, the samples were weighed, and then they were dried. After drying the samples were weighed again and subjected to a CB-X Total Protein Assay.

STATISTICAL ANALYSES

I checked the residuals for each consumption rate variable (separated by sex of the adult) for normal distribution prior to running analyses.

In order to increase data independence, the average of each variable was found for the nestling age (day). This is the case throughout the results unless otherwise noted.

Although some broods did contribute observations to multiple nestling age day averages, the averages came from a different combination of broods for each day.

RESULTS

I analyzed slightly more than 200 hours of video of 23 broods in 19 boxes. Average observation time per brood was 8 hours 42 minutes. The longest net observation time for an individual brood was 16 h: 47 m (Brood 31B), and the shortest was 1 h: 43 m (Brood 17). Adult Eastern Bluebirds were observed handling 372 individual fecal sacs. Female Bluebirds handled 224 of those 372 fecal sacs (60.2 %), males handled 124 (33.3 %). The other 24 (6.5 %) were handled by adults that could not be identified by sex. Of the 372 fecal sacs handled by the bluebirds, 150 (40.3 %) were confirmed consumed (Fig. 3; others may have been consumed just outside of the nestbox or on a nearby tree, outside of the view of the camera). Thus, I report minimum fecal sac consumption rates. Female bluebirds consumed 105 of those 150 fecal sacs (46.9 % of the fecal sacs they handled), males consumed 39 fecal sacs (31.5 % of the fecal sacs they handled), and 6 fecal sacs were consumed by adults that could not be identified by sex.

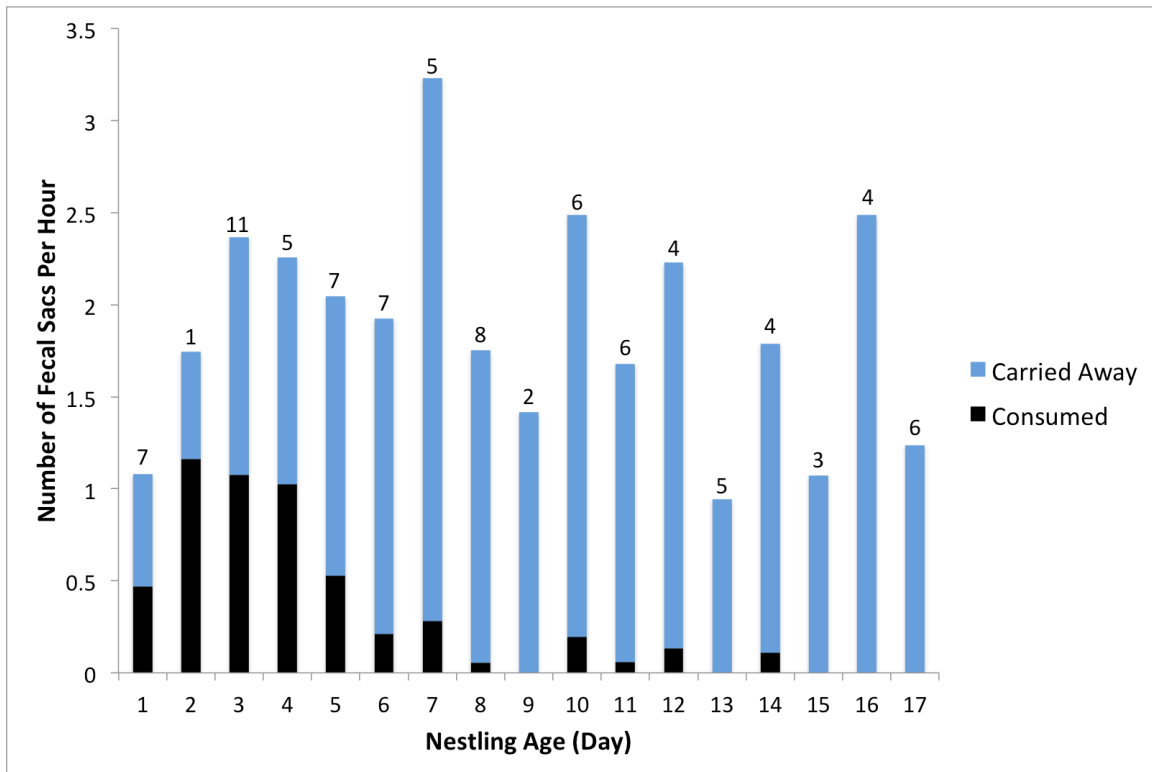


Figure 3. Fecal sac disposal methods (both sexes combined) over the course of the nestling period. Number above bar indicates number of nests.

Both sexes visit the nest and provision nestlings throughout the nestling period (Fig. 4). Females averaged 1.14 provisioning visits per hour per nestling over the entire nestling period, and males averaged 0.87. The three predictions I tested are placed in this context of a high level of biparental care.

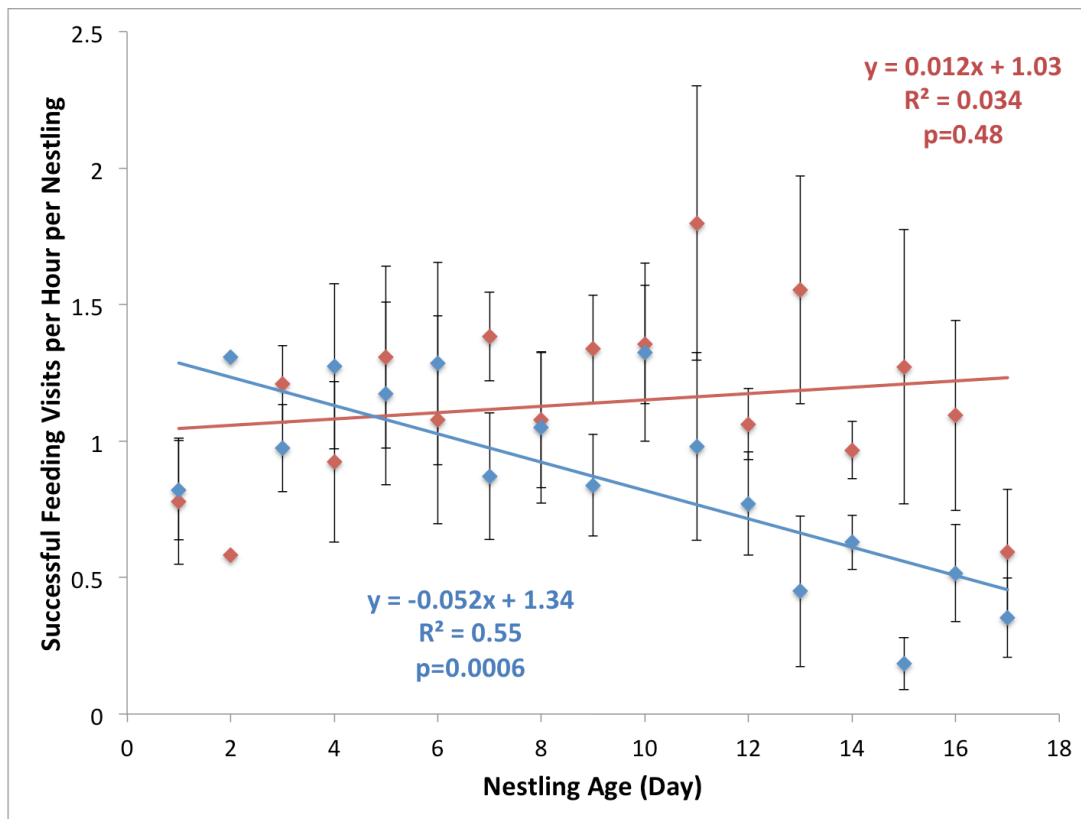


Figure 4. Provisioning rates ($\bar{x} \pm 1$ SE) of male (blue) and female (red) bluebirds as a function of nestling age. Samples sizes are given in Figure 3.

PREDICTION 1

The first prediction to be tested is that adult bluebirds should consume fewer fecal sacs as nestlings age. Fecal sac consumption rates were measured as the number of fecal sacs consumed per hour per nestling because the number of fecal sacs produced is a function of brood size. Fecal sac consumption by both male and female bluebirds declined as nestlings aged (Fig. 5, Table 2). However, examination of Figure 5 shows that the

majority of the decline in fecal sac consumption occurred during the first week of the nestling period (days 1-7), with little change after that point (days 8-17). Figures 6 (females) and 7 (males) show the separate trend lines over these time periods. There were declines in fecal sac consumption early in the nestling period and little change during the latter part of the nestling period.

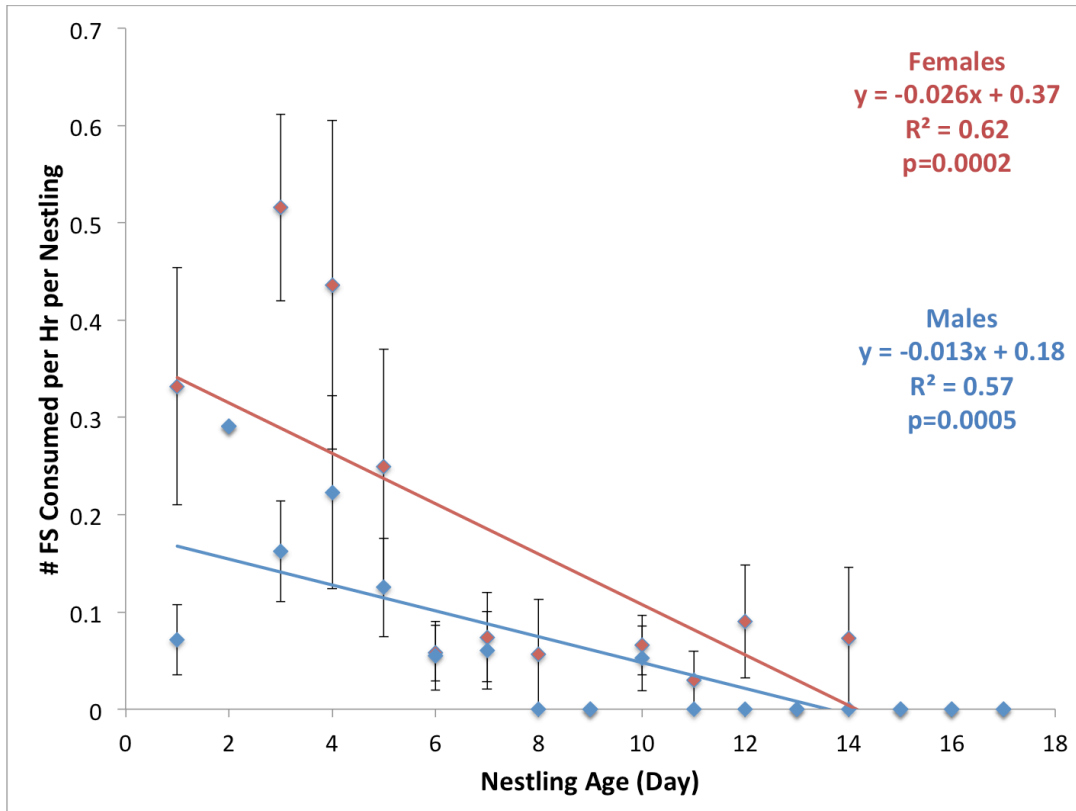


Figure 5. Relationship between fecal sac consumption (# of fecal sacs/hour/nestling) and nestling age for male (blue) and female (red) Eastern Bluebirds. Points are means \pm 1 SE. Sample sizes are given in Figure 3.

The percentage of time per hour that adults spent at the nest was positively correlated with all three measures of fecal sac consumption rates, suggesting that adults were actively waiting on fecal sacs to be produced (Table 3).

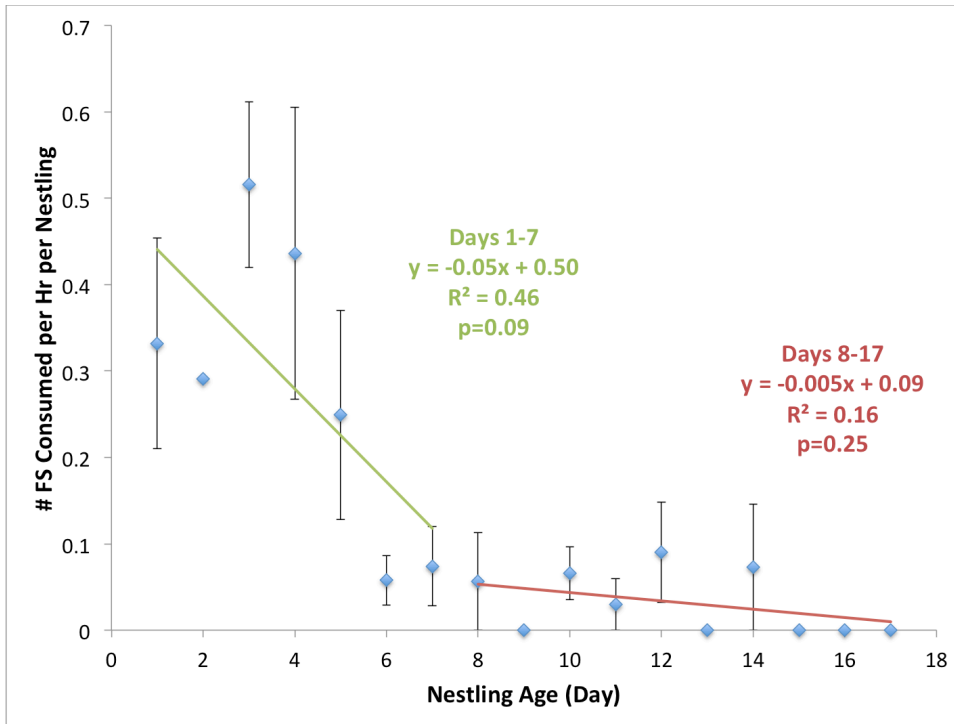


Figure 6. Trends in fecal sac consumption by female bluebirds for nestlings aged 1-7 days and those aged 8-17 days. Points are means \pm 1 SE. Number of nests is indicated in Figure 3.

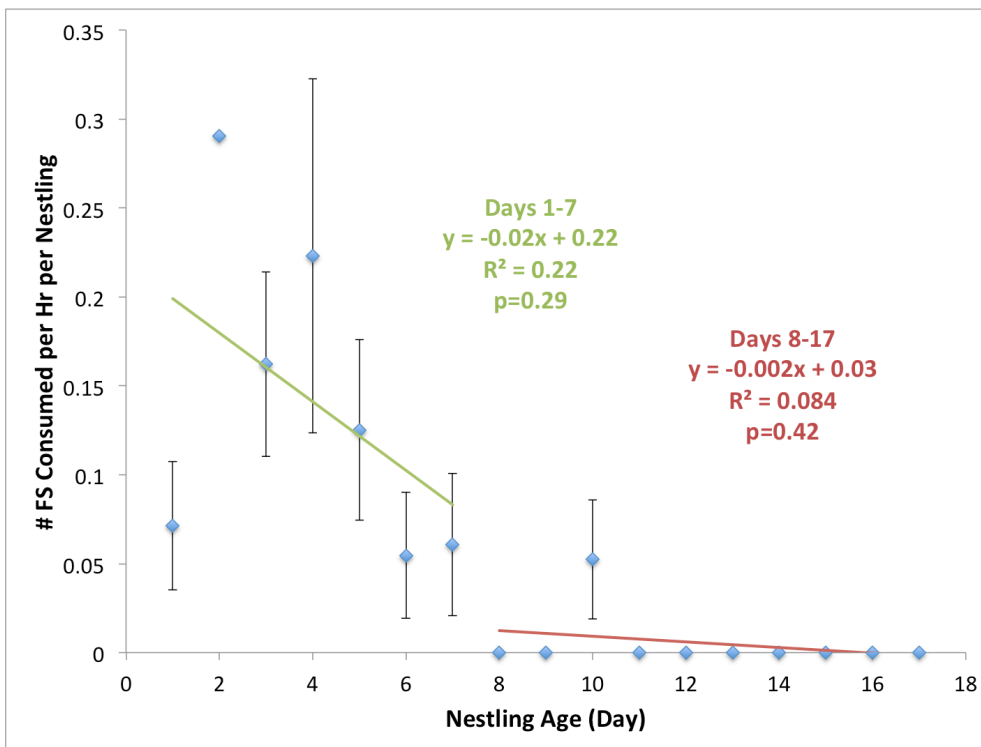


Figure 7. Trends in fecal sac consumption by male bluebirds for nestlings aged 1-7 days and those aged 8-17 days. Points are means \pm 1 SE. Number of nests is indicated in Figure 3.

Table 2. Relationship between measures of investment in male and female Eastern Bluebirds, and characteristics of fecal sacs, as a function of nestling age.

Variable	R ²	p (slope)	Intercept	Slope
Average # FS Consumed per Hour				
Females	0.61	<0.01	1.15	-0.08
Males	0.49	<0.01	0.60	-0.05
Average # FS Consumed per Hour per Nestling				
Females	0.62	<0.01	0.37	-0.03
Males	0.57	<0.01	0.18	-0.01
Average % FS Consumed per Observation Period				
Females	0.69	<0.01	0.87	-0.06
Males	0.74	<0.01	0.90	-0.07
Average Total # Nest Visits per Hour				
Females	0.05	0.38	3.30	0.05
Males	0.47	<0.01	4.24	-0.16
Average Total # Nest Visits per Hour per Nestling				
Females	0.02	0.63	1.13	0.01
Males	0.64	<0.01	1.47	-0.06
Average Successful Feeding Visits per Hour				
Females	0.06	0.34	3.09	0.05
Males	0.40	<0.01	3.97	-0.15
Average Provisioning Rate				
Females	0.03	0.48	1.04	0.01
Males	0.55	<0.01	1.34	-0.05
Average % of Time per Hour Spent at Nest				
Females	0.50	<0.01	0.16	-0.01
Males	0.76	<0.01	0.03	-0.002
Average Total Protein (µg)	0.15	0.12	638.47	-1.23
Average Fecal Sac Dry Weight (g)	0.20	0.07	0.12	0.02
Average Protein (µg per g of fecal sac)	0.32	0.02	47,773.19	-3,416.25

PREDICTION 2

The second prediction I tested was that the nutritional value of fecal sacs should decrease as nestlings age. Total protein per fecal sac did not change significantly as nestlings aged (Fig. 8). However, fecal sacs tended to be heavier as nestlings aged (Fig. 9). As a result, there was a significant decline in the amount of protein per gram of fecal sac as nestlings aged (Fig. 10). Interestingly, the decline in protein content per gram of fecal sac occurs primarily over days 1-7, the same pattern seen in the decline of fecal sac consumption.

PREDICTION 3

The third prediction I tested was that females should consume more fecal sacs than males. As demonstrated earlier (Fig. 5), both males and females consume fewer fecal sacs over time. However, female consumption declines at a faster rate (ANCOVA, $p=0.04$). Over the entire nestling period, females have a higher mean per capita consumption of fecal sacs than males (paired $t = 2.79$, $df = 16$, $p = 0.013$). The same is true for days 1-7 when the most fecal sacs are consumed (paired $t = 2.58$, $df = 6$, $p = 0.042$).

MICRONUTRIENTS

I analyzed a small sample of fecal sacs ($n=6$) for nutrient content. Based on this small sample there were no consistent trends as nestlings aged (Appendix).

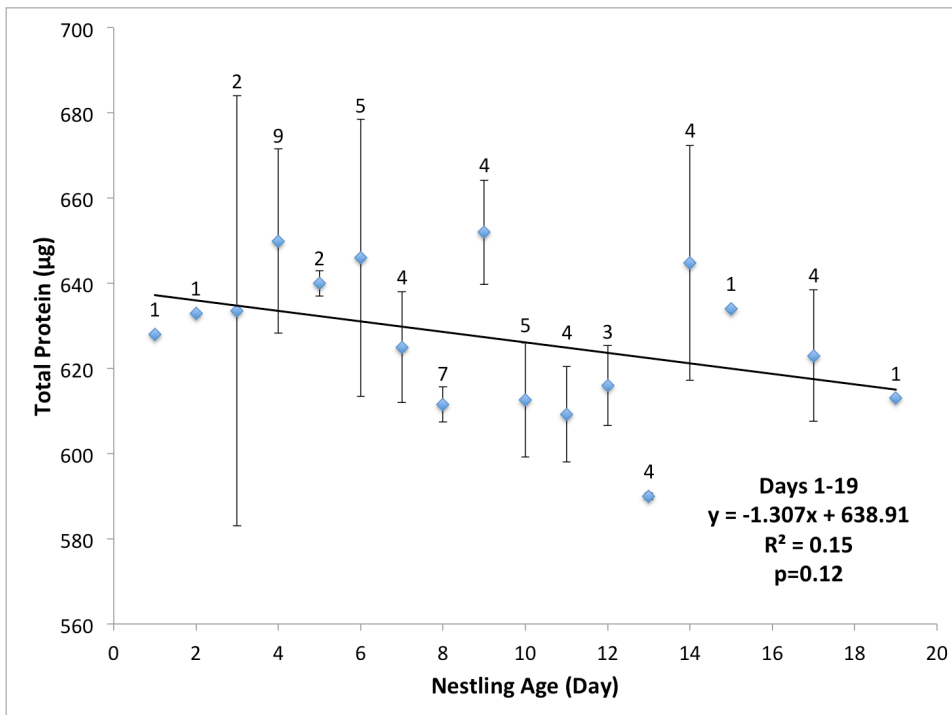


Figure 8. Total Protein (μg) of fecal sacs as a function of nestling age ($\bar{x} \pm 1$ SE). Numbers above bars are sample sizes.

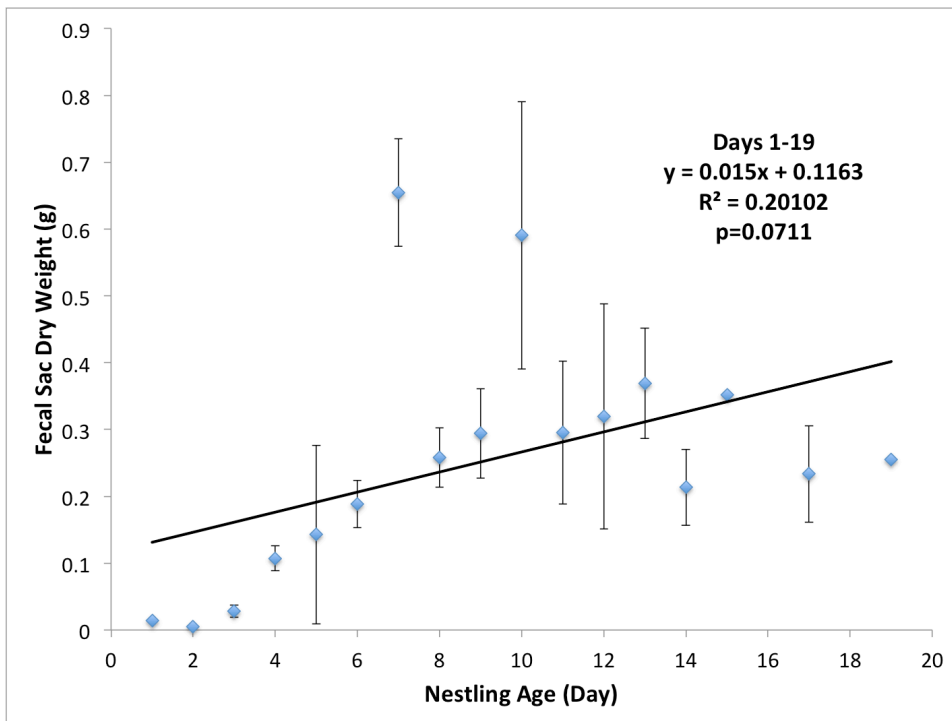


Figure 9. Fecal Sac Dry Weight (g) as a function of nestling age ($\bar{x} \pm 1$ SE). Sample sizes as in Figure 8.

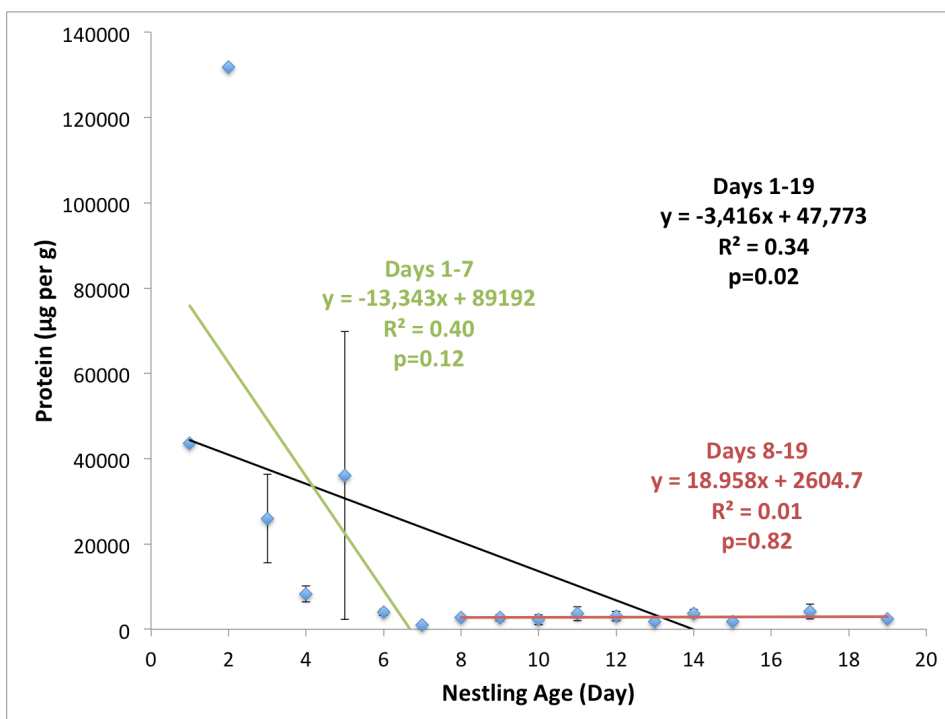


Figure 10. Protein (μg per g of fecal sac) as a function of nestling age ($\bar{x} \pm \text{std error}$). Sample sizes as in Figure 8.

Table 3. Correlation between nest attendance and fecal sac (FS) consumption rates.

Variable (n=17 unless otherwise noted)	Average Percentage of Visits with Prodding	Average Net Length of Nest Visit(s)	Average Percentage of Time per Hour Spent at Nest
Avg # FS Consumed/Hour			
Females	0.74 (p<0.01)	0.61 (p=0.01)	0.67 (p<0.01)
Males	0.47 (p=0.06)	0.30 (p=0.24)	0.68 (p<0.01)
Avg # FS Consumed per Hour per Capita			
Females	0.82 (p<0.01)	0.71 (p<0.01)	0.77 (p<0.01)
Males	0.44 (p=0.08)	0.37 (p=0.15)	0.70 (p<0.01)
Avg % FS Consumed per Observation Period			
Females	0.80 (p<0.01)	0.66 (p<0.01)	0.70 (p<0.01)
Males	0.41 (n=16, p=0.12)	0.64 (n=16, p<0.01)	0.78 (n=16, p<0.01)

DISCUSSION

In summary, my results were consistent with all three of the predictions of the parental nutrition hypothesis that I tested (Fig. 1). Fecal sac consumption rates decreased as nestlings aged for both male and female bluebirds (Table 2, Fig. 5). In fact, fecal sacs were consumed at very low rates after approximately day 7 (Fig. 6 and 7). Perhaps not coincidentally, protein content declined primarily from day 1-7. Measured as protein per gram of material, fecal sacs had little nutritional value after day 7 (Fig. 10). Finally, female bluebirds consumed more fecal sacs than males, at least early in the nestling cycle when fecal sacs had higher relative protein content.

The decrease in fecal sac consumption as nestlings aged was expected based on previous studies (Conder 1948, Glück 1988, Hurd et al. 1991, McGowan 1995, Hagelin et al. 2015). The parental nutrition hypothesis posits that this shift is because of an increase in nestlings' digestive efficiency, which results in a decrease in the nutritional value of fecal sacs. My results support this idea. There was a remarkable congruence between the decline in fecal sac consumption rate and the amount of protein (μg) per gram of fecal sac (Table 5). Both sexes consumed fewer fecal sacs as nestlings aged (Fig. 6 and 7). It is interesting to note that the change occurs primarily during the first week of the nestling period.

Protein is an important nutrient to test as part of the PNH because of the large amount of protein used by females in egg production. There is little protein per gram of fecal sac that must be digested after day 7 (Fig. 10). Male and female bluebirds seem to respond accordingly. There would be advantages to males as well because they have expended energy establishing and maintaining territories. Nevertheless, replacing

nutrients lost during egg-laying should make fecal sacs more valuable to female birds than males from a physiological perspective, and this is a prediction of the parental nutrition hypothesis. My data showed a consistently higher fecal sac consumption rate in female bluebirds than in males (Fig. 5). Thus, all three predictions tested in this study were met by the data, providing additional support for the parental nutrition hypothesis.

To my knowledge there are no published studies concerning the micronutrient content of fecal sacs. Macromolecule nutrient studies are also surprisingly rare. The protein content of fecal sacs has only been investigated once prior to this study; Morton (1979) measured the fat, carbohydrate, and inorganic contents of fecal sacs. Others have investigated the nutritional value of fecal sacs by equating energy with nutrition (Glück 1988, Hurd et al. 1991). This approach is flawed because materials like chitin may not be digestible for birds but would combust in a bomb calorimeter and appear to be available calories (see McGowan 1995).

Calcium is of particular interest when testing the parental nutrition hypothesis because of the critical nutritional role it plays. The diet of insectivorous and granivorous passerines does not provide sufficient calcium for reproduction (Graveland and Van Gijzen 1994). Many species use eggshells, snail shells, and grit as diet supplements during the breeding season. Boreal Chickadees have been observed consuming ash high in calcium, presumably as a diet supplement (Ficken 1989). Calcium's role in a multi-brooded species like the Eastern Bluebird may be of even greater importance. If fecal sacs from nestlings of a certain age can serve as calcium sources, that would provide strong evidence in support of the parental nutrition hypothesis.

Support for the PNH does not mean that nutritional value in fecal sacs is the only thing selecting for fecal sac consumption, but it suggests that fecal sac nutritional value is one viable selection pressure. In fact, the adjustable sanitation hypothesis (Gow et al. 2015) posits that sanitation effort can be altered depending on current conditions. Thus, sanitation effort is not rigidly set, but rather a continuous trade-off between provisioning demands, predation risks, and other pressures that fluctuate throughout the nest cycle. For example, Great tit parents (*Parus major*) spend less time sleeping when their nest is infested with ectoparasites (versus a parasite-free nest) in order to allocate more time to nest sanitation (Christe et al. 1996). Gow et al. (2015) found that Northern Flickers (*Colaptes auratus*) show flexible nest sanitation effort when faced with increased provisioning demands brought on by single-parenthood.

It should be noted that my data are broadly consistent with the economic disposal hypothesis as well. The parental nutrition hypothesis says that consumption of fecal sacs declines as nestlings age because there is less nutrition in the fecal sac. The economic disposal hypothesis explains the same decline as the result of heavier fecal sacs being more costly to digest. My data show both patterns; protein content declines (Fig. 10) and fecal sac mass increases (Fig. 9) as nestlings age from days 1-7. The key question is whether consumption decreases as a result of protein declining, from about 50,000 $\mu\text{g/g}$ to near zero by day 7 (Fig. 10), or whether it is due to the mass increasing by less than 0.1 g by day 7 (Fig. 9). I suggest that the former is the more likely cause, but both factors could be contributing to the observed decline in fecal sac consumption.

FUTURE DIRECTIONS

A full understanding of the benefit of fecal sac consumption will require the examination of several variables. Parental body condition, food availability, weather, age and experience of the adults, sex, clutch size, brood size, mating system, macro- and micro-habitat, and time of year may all play a role in influencing fecal sac consumption behavior habits. It is also possible that the various hypotheses proposed by biologists are not mutually exclusive, and that passerines may employ different strategies for fecal sac disposal as conditions change (Ibáñez-Álamo et al. 2013).

Studying fecal sac consumption does not seem to be a popular area of inquiry, and as a result the modern body of data (i.e., not including observations from Thomson 1934, Blair and Tucker 1941, Tucker 1942, Smith 1942) is limited to 23 species of birds. To my knowledge, fewer than 20 peer-reviewed papers related to the adaptive nature of fecal sac consumption have been published over the last 48 years. In addition, only three experimental studies have been conducted (Petit et al. 1989, Ibáñez-Álamo et al. 2013, Gow et al. 2015); the rest are observational. This lack of data makes it difficult to draw conclusions that reach any further than an individual species in regard to whether nutrition, economy, satiation, or predation is the primary selective pressure behind a parent bird's method of disposal. There are lines of inquiry that might yield important insights.

For example, fecal fat microscopy (Fine and Ogunji 2000) could yield additional insight into the nutritional value of fecal sacs without the expense of analyzing samples through a third party laboratory and without the relative expertise required for more

complex assays. Investigating the amount of time an adult spends waiting for a just-fed nestling to void a fecal sac may provide insight into the importance of the potential nutritional value within the fecal sac; one could speculate that if an adult passerine spends more time waiting for a fecal sac, the adult is in greater need of nutritional supplement/s. However, waiting a longer period of time for a fecal sac may also imply a stronger drive towards maintaining nest sanitation. Likewise, prodding habits may give clues about parental nutrition needs and/or nest sanitation as a priority. In order to distinguish prodding and waiting behaviors as being motivated by nest sanitation or nutritional needs, perhaps one could attempt to correlate an individual passerine's retrieval habits with its consumption habits. There are several peer-reviewed papers (e.g., Studier and Sevick 1992, Robel et al. 1995, Barker et al. 1998) that quantify the nutritional contents of various orders of insects. These resources could perhaps be used along with high-quality camera recordings of food items fed to nestlings to estimate nestling digestive efficiency with minimal disturbance to the nest and without invasive procedures.

Ultimately, there are a multitude of questions that still need to be asked regarding the existing hypotheses. For example, if McKay's parental satiation hypothesis is correct, are adults who have recently consumed a fecal sac less likely to consume a second one? On at least a couple of occasions observed via my video recording fecal sac consumption was influenced by the presence of a second fecal sac: after feeding a nestling, the adult picked up a fecal sac that had been hidden previously or had been voided in its absence, and a nestling voided a fresh fecal sac while the adult had the first one in its beak, forcing the adult to swallow the older one so that it could retrieve the newer one. Also, will adults who have consumed a fecal sac within the last, say, 10 or 15 minutes wait a shorter

amount of time after feeding a nestling to see if it voids a fecal sac? Do instances of insistent prodding correspond at all with the amount of nest attendance time or the time since the last fecal sac was consumed?

REFERENCES

- Barker, D., M.P. Fitzpatrick, and E.S. Dierenfeld. 1998. Nutrient composition of selected whole invertebrates. *Zoo Biology* 17:123-134.
- Blair, R.H., and B.W. Tucker. 1941. Nest sanitation. *British Birds* 34:206-215, 226-235, 250-255.
- Calder, W.A. 1968. Nest sanitation: a possible factor in the water economy of the Roadrunner. *Condor* 70:279.
- Calvo, B., and R.W. Furness. 1992. A review of the use and the effects of marks and devices on birds. *Ringling & Migration* 13:129-151.
- Caviedes-Vidal, E., and W.H. Karasov. 2001. Developmental changes in digestive physiology of nestling House Sparrows, *Passer domesticus*. *Physiological and Biochemical Zoology* 74:769-782.
- Christe, P., H. Richner, and A. Oppliger. 1996. Of Great Tits and fleas: sleep baby sleep . . . *Animal Behaviour* 52:1087-1092.
- Cliburn, J.W. 1978. Disposal of fecal sacs in water by Common Grackles. *Mississippi Kite* 8:12.
- Conder, P.J. 1948. The breeding biology and behavior of the Continental Goldfinch *Carduelis carduelis carduelis*. *Ibis* 90:493-525.
- Dell'Omo, G., E. Alleva, and C. Carere. 1998. Parental recycling of nestling faeces in the common swift. *Animal Behaviour* 56: 631-637.
- Ficken, M.S. 1989. Boreal chickadees eat ash high in calcium. *Wilson Bulletin* 101:349-351.

- Fine, K.D., and F. Ogunji. 2000. A new method of quantitative fecal fat microscopy and its correlation with chemically measured fecal fat output. *Clinical Chemistry* 113:528-534.
- Glück, E. 1988. Why do parent birds swallow the feces of their nestlings? *Experientia* 44: 537-539.
- Gow, E.A., K.L. Wiebe, and A. Musgrove. 2015. Nest sanitation in response to short- and long-term changes of brood size: males clean more in a sex-role reversed species. *Animal Behaviour* 104:137-143.
- Graveland, J., and T. Van Gijzen. 1994. Arthropods and seeds are not sufficient as calcium sources for shell formation and skeletal growth in passerines. *Ardea* 82:299-314.
- Hagelin, J.C., S. Busby, A. Harding-Scurr, and A.R. Brinkman. 2015. Observations on fecal sac consumption and near-ground foraging behavior in the Olive-sided Flycatcher (*Contopus cooperi*). *Wilson Journal of Ornithology* 127:332-336.
- Herrick, F.H. 1900. Care of nest and young. *Auk* 17:100-103.
- Hurd, P. L., P. J. Weatherhead, and S. B. McRae. 1991. Parental consumption of nestling feces: good food or sound economics? *Behavioral Ecology* 2: 69-76.
- Ibáñez-Álamo, J.D., O. Sanllorente, L. Arco, and M. Soler. 2013. Does nest predation risk induce parent birds to eat nestlings' fecal sacs? An experimental study. *Annales Zoologici Fennici* 50: 71-78.
- Lang, J. D., C. A. Straight, and P. A. Gowaty. 2002. Observations of fecal sac disposal by Eastern Bluebirds. *Condor* 104: 205-207.

- McGowan, K. J. 1995. A test of whether economy or nutrition determines fecal sac ingestion in nesting corvids. *Condor* 97: 50-56.
- McKay, J. E., M. T. Murphy, S. B. Smith, and J. K. Richardson. 2009. Fecal-sac ingestion by Spotted Towhees. *Condor* 111: 503-510.
- Møller, A.P. 1993. Ectoparasites increase the cost of reproduction in their hosts. *Journal of Animal Ecology* 62:309-322.
- Morton, M. L. 1979. Fecal sac ingestion in the Mountain White-crowned Sparrow. *Condor* 81:72-77.
- Petit, D. R., and L. J. Petit. 1987. Fecal sac dispersal by Prothonotary Warblers: Weatherhead's hypothesis re-evaluated. *Condor* 89: 610-613.
- Petit, K. E., L. J. Petit, and D. R. Petit. 1989. Fecal sac removal: do the pattern and distance of dispersal affect the chance of nest predation? *Condor* 91: 479-482.
- Robel, R.J., B.M. Press, B.L. Henning, and K.W. Johnson. 1994. Nutrient and energetic characteristics of sweepnet-collected invertebrates. *Journal of Field Ornithology* 66: 44-53.
- Skutch, A.F. 1976. *Parent birds and their young*. University of Texas Press, Austin.
- Smith, S. 1942. The instinctive nature of nest sanitation. *British Birds* 35:120-124, 186-188.
- Studier, E.H., and S.H. Sevick. 1992. Live mass, water content, nitrogen and mineral levels in some insects from south-central lower Michigan. *Comparative Biochemistry and Physiology* 103:579-595.
- Trivers, R.L. 1972. Parental investment and sexual selection. Pp. 136-179, Campbell, B. (ed.). *Sexual selection and the descent of man, 1871-1971*. Aldine, Chicago.

Tucker, B. W. 1942. Further data on nest sanitation. *British Birds* 35: 66-72, 90-97.

Weatherhead, P. J. 1984. Fecal sac removal by Tree Swallows: the cost of cleanliness.

Condor 86: 187-191.

Welty, J. C., and L. Baptista. 1988. *The life of birds*. Saunders College Publishing, New York.

APPENDIX

Micronutrient content (ppm/mg) of six fecal sacs taken from nestlings of six different ages.

Micronutrient (ppm/mg)	2	Nestling 3	Age 4	10	11	13
Calcium	678.52	46.43	44.78	7,380.72	43.60	950.28
Ammonium	239.91	955.52	830.11	1,108.56	1,534.26	1,396.26
Potassium	9,251.58	1,220.86	3,045.49	7,269.03	5,029.84	6,725.11
Magnesium	756.75	321.23	211.48	1,906.27	640.98	469.43
Sodium	2,261.41	1,563.19	3,568.1	190.20	1,374.31	974.01