

Brood Size dependent differences in Prey Delivery rates among Flammulated Owls
(*Psiloscops flammeolus*)

A Senior Thesis Presented to
The Faculty of the Department of Biology,
The Colorado College

By

Bryan Grundy

Bachelors of Arts Degree in Biology

19th day of May, 2014

Dr. Brian D. Linkhart
Primary Thesis Advisor

Dr. Marc Snyder
Secondary Thesis Advisor

Abstract

Optimal clutch size has been an important focus within evolutionary biology since David Lack's innovative work in 1947. Prey abundance, typically thought to limit clutch size, may be especially limiting in raptors, since the females contribute minimally to prey provisioning. Studying species with significant energetic constraints may illuminate the relationship between energetics, parental division of labor and clutch size. Flammulated Owls (*Psiloscops flammeolus*) are a small raptor with prey that is small relative to their body size, further constraining flammulated owls energetically when compared to raptors with larger prey. I hypothesized that female flammulated owls with clutches of three will contribute more to prey deliveries than females with clutches of two, while male prey delivery rates will not vary with brood size. Prey delivery data from 115 flammulated owl nests in the Front Range of Colorado were recorded from 2004-2013. During the second half of the nestling period broods of three received more prey deliveries than broods of two ($p < 0.05$). Additionally, during the second half of the nestling period no significant difference was found between male and female prey delivery rates for broods of three ($p > 0.05$). However, among adults with broods of two, males provided significantly more prey than females ($p < 0.05$). Male prey delivery rate between brood sizes was not significantly different ($p > 0.05$). These results indicate that broods of three may require greater energy expenditure than broods of two from the female, but not the male parent. While these results pertain to a bird with a small inflexible clutch size, similar research on birds with larger more flexible clutch sizes may reveal how and if clutch size and parental division of labor have co-evolved within avian taxa.

Introduction

The number of offspring an individual produces during a single reproductive effort has been an important focus within evolutionary biology and one of the best-studied life history traits since David Lack's innovative work on avian clutch size in 1947. Lack (1947) proposed that clutch size is limited by the amount of prey parents can provide their offspring and, due to natural selection, the clutch size that produces the most fledglings should be the most common. Clutch size, unlike most parameters affecting fitness, is heritable (van Noordwijk and van Balen 1988, Newton 1989). In accordance with Lack's (1947) hypothesis, there has been little evidence of continued clutch size selection, except in recently established bird populations (Tinbergen and Sanz 2004). However, in contrast with Lack's (1947) hypothesis, studies have indicated that the clutch size producing the most fledglings is often larger than the most common clutch size (Perrins 1965, Cave 1968, Perrins and Moss 1975, De Steven 1980, Nur 1984).

Since Lack's (1947) work, scientists have shown that the number of fledglings produced in a single breeding attempt gives an incomplete look at parental fitness, in part, because it does not take into account future reproductive success of the parents (Williams 1966). Cody (1966) proposed that the amount of energy a bird can expend throughout its lifetime is finite. As such, there is a trade off between current and future reproductive success (Ghalambor et al. 2001). Lifetime reproductive success (LRS)—the number of fledglings or recruits an individual produces throughout their lifetime—gives a far more accurate estimate of fitness than a single breeding attempt (Newton 1989). As such, Lack's (1947) hypothesis is best applied to animals that exhibit semelparity, since there is

no tradeoff between current and future reproductive success in these species (Godfray et al. 1991).

The costs to future reproductive success were proposed as elements of clutch size theory posited by Williams (1966) and later by Charnov and Krebs (1974), but were not supported empirically until more recently. Initial studies failed to detect a parental cost, but researchers only manipulated brood size and did not account for the costs of incubation (Korpimäki 1987, Dijkstra et al. 1990), which was thought to be less costly than brooding (Monaghan and Nager 1997). Researchers accounting for incubation, through experimentally enlarged clutches, have found decreases in future fecundity of the parents (Hanssen et al. 2005) and decreased parental survival (Visser and Lessels 2001). However, other studies that accounted for incubation have failed to find a cost from increased clutch size (Tinbergen and Sanz 2004).

In addition to the direct parental costs of increased clutch size, there appear to be delayed costs to offspring and thus parental fitness. Large clutches have been linked with a lower overwinter survival rate in young, minimizing any evolutionary advantage towards large clutch sizes (Lindén and Møller 1989, Styrsky et al. 2005). Gustafsson and Sutherland (1988) also found that young from experimentally enlarged collared flycatcher (*Ficedula albicollis*) clutches had lowered fecundity compared with control broods. While these studies indicated a cost for experimentally enlarged broods, they did not provide evidence for selection against large brood sizes. However, they did indicate the potential for parent-offspring conflict, as costs are not necessarily equally distributed between parents and offspring. In longer-lived species parental survival should be

avored over offspring survival, while in shorter-lived species offspring survival may be prioritized, minimizing conflict (Lindén and Møller 1989).

Conflict over parental investment and clutch size does not only occur between parents and offspring—it can also occur between the male and female parent when there is unequal investment in offspring. While the effect of clutch size on parental investment and division of labor has not been a primary focus of most clutch size studies, a number of studies using raptors have examined this issue (Olsen et al. 1998, Leckie et al. 2008). Division of labor is especially unequal among species that exhibit reverse sexual size dimorphism (RSSD), including raptors, where males are largely responsible for providing prey while females are the sole incubators and brooders (Holthuijzen, 1990). Though female raptors contribute little to prey deliveries, especially early in the nestling period, their contribution generally increases with nestling age (Newton 1979). The female's increase in prey delivery rate is rendered possible by a decreased need for brooding as young become homeothermic and is important in some species, as nestling energy requirements increase with nestling size (Newton 1979). In some species female contribution increased with nestling age, but did not increase with brood size, though male provisioning did increase with brood size (Newton 1986, Masman et al. 1989, Tolonen and Korpimäki 1994, Olsen et al. 1998). Hen harriers (*Circus cyaneus*) are a known exception, with female prey delivery rate increasing with brood size (Leckie et al. 2008).

Raptor clutch size is likely heavily constrained by having one parent provide the majority of prey, since even in avian taxa where both sexes contribute similarly to the energetic needs of the nest, prey is still regarded as the limiting factor (Lack 1954).

Clutch size is further constrained by the fact that raptors are single-prey-loaders—they can only deliver one prey item to the nest at a time, unlike birds in many avian taxa where an individual can bring several prey items at a time (Sonerud 1992). In order to offset these limitations, many raptors catch large prey relative to their body size.

Studying a raptor that catches relatively small prey—one that has not adapted to avoid these constraints—may provide greater insight into the relationship between energetics and clutch size.

Flammulated owls (*Psiloscopus flammeolus*) are a small species of raptor that prey primarily on arthropods, which weigh well under one percent of the mass of an adult flammulated owl (Linkhart, *pers. comm.*). As raptors, they are single prey loaders and provisioning their young requires frequent flights due to their small prey size. These flights represent a substantial energy expenditure on the part of the male, with males losing approximately 20% of their body mass over the course of the nestling period (Linkhart, *pers. comm.*). They are obligate secondary cavity nesters with males providing for a single clutch of between one and four eggs, though most clutches consist of two or three eggs (Linkhart and McCallum, 2013).

While clutch size is often limited by prey availability, in some species, other factors such as predation, (Skutch 1949, Slagsvold 1982) and in secondary cavity nesters, nest size (Löhrl 1973), prove limiting. However, I do not think that these additional factors significantly affect clutch size in flammulated owls for reasons I will detail below. Cavity size does not appear limiting as, northern flickers, the primary excavators of cavities used by flammulated owls, are larger, have larger clutches and fledge more young than flammulated owls (Wiebe and Swift, 2001). While predation can limit clutch

size due to increased detection of larger broods (Skutch 1949), cavity nesting generally lowers predation. Additionally, the primary nest predators of flammulated owls are diurnal, minimizing increased detection of larger broods.

Considering their constraints as raptors and the additional constraint of small prey, prey availability likely plays the most important role in determining flammulated owl clutch size. As is common in raptors, female flammulated owls brood the young while the male is almost solely responsible for feeding the nestlings and the female during the first twelve days of the nestling period (Reynolds and Linkhart 1987). After this period the nestlings are homeothermic and the female begins foraging and bringing prey to the nestlings.

Prior research on flammulated owls suggests that broods of three require more energy than broods of two, as broods of three reach a higher asymptotic mass prior to fledging than broods of two (Jones 2012). To better understand the relationship between energetic constraints and brood size, I looked at prey delivery rates as an indicator of both parental effort (Tolonen and Korpimäki 1994) and the energetic needs of the young, throughout the nestling period. While Tolonen and Korpimäki (1994) questioned the use of prey deliveries as a surrogate for parental effort in male kestrels (*Falco tinnunculus*), I think that prey deliveries provided a suitable estimate of parental effort in flammulated owls. Unlike kestrels, which frequently hover while hunting (Masman et al. 1989), flammulated owls typically hunt from a perch (Linkhart and McCallum 2013). Additionally, while prey size can increase with brood size in some raptor species (Newton 1986), observations suggest that there is little variance in flammulated owl prey size (Linkhart, *pers. comm.*). First I hypothesized that prey delivery rates will be lower

per nestling in broods of three than in broods of two during the first half of the nestling period. Second, during the second half of the nestling period, nestlings in broods of three will receive, on average, equal prey delivery rates per nestling as their counterparts in broods of two. Third, female owls will be responsible for this predicted higher rate of per nest prey deliveries in broods of three, as males will be unable to increase their contribution.

Methods

Natural History

Despite weighing less than seventy grams, the life history of flammulated owls bears strong similarities to those of large raptors (Linkhart and Reynolds 2004). Males have been known to breed for at least fourteen years, while females do not appear to breed for as long (Linkhart and Reynolds 2004). The owls breed from southern Mexico, and possibly farther south, to southern Canada (Linkhart and McCallum 2013). Migration to breeding sites occurs in late spring and migration to wintering grounds located in Mexico and Central America occurs in early fall (Linkhart and McCallum 2013).

Incubation lasts for an average of twenty-two days and begins once the penultimate egg has been laid. Following hatching, which is asynchronous, the nestlings remain in the nest for an average of twenty-three days in the Colorado Front Range population (Linkhart and Reynolds 1987). Upon fledging it appears that broods are usually split between the male and female, with the male caring for the first two to fledge in broods of three while the female cares for the third fledgling (Linkhart and Reynolds 1987a).

Study Sites

Prey delivery data were collected in four study areas located within Teller County, Colorado, between 2550 and 2855m in elevation (Linkhart et al. 2007). Data were collected during June and July, the nesting season for flammulated owls, from 2004-2013 (Linkhart, *unpubl. data*). Additional data on owlet development, nesting success and chronology were collected in the same study areas from 1981-2013 (Becker 2008, Jones 2012). The majority of data were collected in two study areas, the Hotel Gulch Study Area (HGSA) and the Missouri Gulch Study Area (MGSA), within the Manitou Experimental Forest (MEF). The HGSA, where the study began, is 5.5km² and has had an average of eight territories occupied by breeding pairs (Linkhart, *unpubl. data*), while the MGSA, which has been studied since 2002, is 6km² and has supported an average of ten breeding territories from 2004-2013. Males have a 92% territory fidelity, with females showing lower, but still relatively high fidelity following a successful nesting attempt, but very low fidelity following an unsuccessful attempt (Linkhart et al. 2007). Territories without nests may be due to a male-biased sex ratio in the adult population (Linkhart and McCallum 2013).

Within these two study sites four forests types cover approximately three quarters of the total area. The ridge tops and southern slopes, which make up 35% of the study area, are comprised of mature ponderosa pines (*Pinus ponderosa*) mixed with Douglas-fir (*Pseudotsuga menziesii*), east and west facing slopes (23%) consist of Douglas-fir (*Pseudotsuga menziesii*), north slopes (8%) have Douglas-fir (*Pseudotsuga menziesii*) and blue spruce (*Picea pungens*), while lower drainage bottoms (8%) support quaking

aspen (*Populus tremuloides*) mixed with blue spruce (*Picea pungens*) (Linkhart et al., 2007).

The Hayman Fire Study Area (HFSA), which burned in 2002 consists of a mix of old growth forest similar to that found in the MEF, along with areas exhibiting a wide range of burn intensities. We began research here in 2004, in the scattered patches of unburned and lightly burned forest that can still support flammulated owls. In most cases territories are not adjoining and many are infrequently occupied, but a mean of five nesting pairs have been located each year. The last study site, the Trout Creek Study Area (TCSA) is 4.5km² and consists largely of secondary growth forest that is similar in species composition to the study areas within the MEF. We have only conducted research in the TCSA since 2008 and in that time a mean of just over three nests have been located each year.

Locating Nests

Trees with known cavities have been flagged and tagged and information on the number and suitability of cavities has been recorded since the beginning of the study. Suitability was determined on the basis of entrance diameter (minimum diameter 4cm), depth (minimum depth 10cm) and flat bottomed (Reynolds and Linkhart 1984). From the onset of incubation, late May, until mid-late July, by which time owlets have fledged, students and researchers systematically searched for nests, through the tapping of cavity trees and examination of cavity contents with pole cameras (Reynolds and Linkhart 1984, Linkhart et al. 1998). We identified territories, which remain fairly constant, through spot-mapping and radio telemetry (Linkhart et al. 1998). We also identified nests during

nighttime searches by listening for nesting vocalizations and using playback to locate territorial males. When we were unable to locate a nest at night, following territorial vocalizations, we re-examined the cavities within the territory. We did not locate nests following all territorial behavior, but as bachelor males appear to be common, we are quite certain that we located the vast majority of nests.

Prey Delivery Observations and Sex Determination

Reynolds and Linkhart (1987) found that prey delivery rates are relatively high following incubation before declining and remaining at a low level for the remainder of incubation, before increasing during the nestling period and peaking just prior to fledging. They also found that prey delivery rates peaked shortly after the start of activity and again in the hour before sunrise. In this paper I define the start of activity as the first appearance of the male in the nest site after sunset, which occurred on average, twenty-three minutes after sunset (Linkhart, *unpubl. data*).

We made prey delivery observations by watching the nest with binoculars from a position where the nest tree was silhouetted against the sky, so that we could observe the adults entering the nest with prey. We made most observation during the first three hours of activity, approximately 8:45pm to 11:45pm. However, the owls remain active throughout the night, with a peak in activity shortly after sunset and another peak shortly before sunrise (Linkhart, *pers. comm.*). Observations were made under a variety of conditions, from relatively unobtrusive monitoring by a single seated observer, to observations made while a capture of one of the adult owls was being attempted. In these instances one researcher stood at or near the base of the nest tree with a telescoping pole

with a net on the end, while a second researcher recorded prey deliveries from nearby. When a prey delivery was attempted, the researcher would cover the cavity with the net after the owl entered, so as to catch the owl as it left the nest.

If the prey delivery rate appeared to be greatly affected by the capture attempt these data were not included in the final analysis. Data were excluded when the number of aborted prey delivery attempts exceeded the number of successful prey deliveries, when four or more aborted prey deliveries occurred during a fifteen-minute interval or if one of the observers noted that one of the adult owls was in the nest site but would not approach the nest. There were likely instances when such an owl went undetected.

Prey deliveries usually consisted of the male or female owl entering the cavity for several seconds before exiting. Arthropod size and order were rarely determined, as lights were generally not used to minimize disturbance. In some cases, usually with owls that had been captured before, they would not fully enter the cavity, but would instead perch on the lip of the cavity and only stick their heads inside to deliver the prey. In some of these instances we were unsure if the delivery had occurred. When we were uncertain for two or more or at least half of prey deliveries during a fifteen-minute period, the data were excluded.

While flammulated owls do exhibit moderate RSSD, they are monomorphic and it was not possible to determine sex based on appearance (Linkhart and McCallum 2013). However, in some cases we were able to determine the sex of the owl making the prey delivery. This determination was often made from hearing the bird vocalize before or after entering the cavity. Sometimes the owls would not continue to vocalize during

subsequent prey deliveries, but the male and female owl would exit and enter the nest site from different but consistent directions, allowing us to accurately determine sex.

Data Organization and Analysis

In total, 3556 prey deliveries were observed at 156 nests over 302 hours (Table 1). Data were sorted into fifteen-minute intervals with the first interval beginning at the start of activity (Linkhart, *unpubl. data*). When at least eleven minutes of an interval were complete I extrapolated to fifteen minutes, but did not retain samples with fewer than eleven minutes of data for statistical analyses. In order to have enough data for statistical comparisons, I grouped fifteen-minute intervals into hour blocks for each of the first three hours of activity. For statistical analyses I used only the mean of all the samples from each nest, so that each nest was represented equally. Due to a lack of normality when data were grouped by day of the nestling period, I grouped data from the first twelve days of the nestling period together and data from the last twelve days, when comparing brood sizes to test my first two hypotheses. When comparing prey delivery rate by sex, I only grouped and analyzed the last twelve days of the nestling period in order to comply with the assumptions of ANOVA. I only used data from the first hour of activity in my analysis, as this hour coincided with the peak in energy requirements of the nest and sufficiently high sample sizes. I used Minitab® 16 (Minitab Inc., State College, PA) to perform general linear model analysis of variance (GLM ANOVA) for comparing prey delivery rates between broods and sexes. I used Levene's test to test for homoscedasticity and the Anderson-Darling test to test for normality. For all tests, results were considered significant when $P < 0.05$. In the results, means are presented with

± 1 standard error (SE). Figures and Tables were created using Excel 2011 (Microsoft Corp., Redmond, WA).

Results

Clutch Size and Fledging Success

To provide necessary context for understanding the prey delivery data, the results of which I will present later, I have included data on the frequency and productivity of different clutch sizes in flammulated owls. The majority of females laid a clutch of three, which was more productive than the other common clutch size of two. Of 209 nests within the study areas, there were five (2.4%) clutches of one, sixty-six (31.6%) clutches of two, 133 (63.6%) clutches of three and five clutches of four (2.4%). The mean number of young fledged for a clutch of one was 0.25 ± 0.25 , 1.08 ± 0.12 for clutches of two, 1.82 ± 0.11 for clutches of three and 3.00 ± 0.41 for clutches of four.

General Patterns

Before presenting the results of my hypothesis testing, here, I present some general patterns in the prey delivery data, which indicate the times within the nestling period and the night the energetic demands of the nest were highest. Mean prey delivery rate, from the whole nestling period was 4.57 ± 0.12 prey deliveries per fifteen minutes (PDs/15min) and generally increased throughout this period. During the first hour of activity, prey delivery rate increased from a mean of 3.48 ± 0.94 PDs/15min on days zero through two, to a mean of 7.77 ± 0.87 PDs/15min on days twenty-one to twenty-three when looking at all brood sizes and both male and female contribution (Figure 1). Prey

delivery rates were generally lower after the first hour, with second and third hour peaks being roughly equivalent to the days of lowest activity during the first hour. During the second hour and third hours of activity, prey delivery rates peaked at 3.80 ± 0.60 and 3.24 ± 0.55 PDs/15min, respectively (Figure 2).

Trends by Brood Size

The results of my first hypothesis test were inconclusive, with the data indicating a trend towards lower prey delivery rates per nestling during the first half of the nestling period when the females were brooding the nestlings. Prey delivery rate per nestling was 1.82 ± 0.32 PDs/15min in broods of two and 1.37 ± 0.24 PDs/15min in broods of three. While the one-way ANOVA test showed no significant difference between brood sizes, it did show an increase in prey delivery rate throughout the nestling period in broods of three ($F = 5.89$, $df = 3$ and 95 , $P < 0.001$, Figure 4). The mean prey delivery rates of broods of two and broods of three were very similar during the second half of the nestling period. Nestlings in broods of three received a mean of 2.75 ± 0.24 PDs/15min and nestlings in broods of two received 2.38 ± 0.52 PDs/15min (Figure 4). Parents of broods of three also brought significantly more prey deliveries per nest during this interval, at 8.25 ± 0.73 (range = 0-24) PDs/15min, than broods of two, which received 5.36 ± 0.65 (range = 0-25) PDs/15min ($F = 10.05$, $df = 3$ and 95 , $P < 0.001$, Figure 5). Fewer data were available for comparisons during the second and third hours of activity, but prey delivery rate appeared higher in broods of two, with 4.74 ± 0.265 (range = 0-14) PDs/15min, than in broods of three, with 3.00 ± 0.235 (range = 0-11) PDs/15min, on days twelve to nineteen of the nestling period (Figure 7 and Figure 8). During other portions of the

nestling period, during the second and third hours of activity, there did not appear to be differences in prey delivery rates between broods of two and broods of three.

Sex-based differences in Prey Deliveries

My third hypothesis was not supported as females with broods of three did not bring prey at a higher rate than their counterparts with broods of two. However, males providing for broods of three did not have higher prey delivery rates than females with broods of three, while in broods of two there was a significant difference between sexes ($F = 6.77$, $df = 3$ and 94 , $P < 0.001$, Figure 6). These findings suggest, albeit indirectly, that female rate may be higher in broods of three than in broods of two. Females with broods of two brought a mean of 1.32 ± 0.33 (range = 0-7) PDs/15min and females with broods of three brought 2.26 ± 0.37 (range = 0-11) PDs/15min. Males with broods of two brought a mean of 3.19 ± 0.64 (range = 0-21) PDs/15min, which was not significantly different than the rate of males with broods of three, which brought a mean of 4.50 ± 0.61 PDs/15min (range = 0-17).

Discussion

My first hypothesis was not fully supported by the data, which indicated a trend towards fewer prey deliveries per nestling in broods of three than broods of two during the first part of the nestling period. During the second half of the nestling period, when females could contribute to prey deliveries, there were no differences in per nestling prey delivery rates between brood sizes. Prey delivery rates per nest were higher in broods of three than in broods of two, supporting my second hypothesis. Since this relative increase

began at the start of female contribution, I expected that female rate was higher in broods of three than in broods of two, while male rate did not vary with brood size. However, neither male nor female prey delivery rates were significantly higher in broods of three than in broods of two, despite the fact that overall rate was higher in broods of three. More data will be necessary to determine which of the sexes, if not both, had a higher prey delivery rate in broods of three than in broods of two.

My findings appear to be consistent with Jones's (2012) findings, which indicated that rate of nestling mass gain in broods of three was initially slower than in their counterparts in broods of two, but by fledgling, nestling from broods of three had a higher asymptotic mass than those from broods of two. Based on prey delivery rates during the first hour of activity and nestling mass, it appears that there is little to no disadvantage to nestlings in broods of three compared to those in broods of two. Given the apparent success of broods of three, it is surprising that this clutch size is the maximum commonly occurring clutch size. The relative absence of clutches of four may be explained by survival and costs outside of the nestling period.

Thompson et al. (2001) suggest that the number of nestlings to fledge is not necessarily correlated with the number of nestlings that will survive to breed. Though very few clutches of four have been documented, the proportion of young to fledge from these nests does not appear lower than the proportion from clutches of three. However, following fledging, male and female flammulated owls may not be able to affectively divide four fledglings between them. During the first five days of the fledgling period the fledglings cannot hunt nor fly well (Linkhart and Reynolds 1987). During this period, the female, the heavier of the two parents, may not be able to efficiently make the required

flights to feed two fledglings. In Eurasian sparrowhawks (*Accipiter nisus*) the females in some pairs do not contribute anything to the feeding of fledglings (Eldegard et al. 2003), suggesting that this activity may be costly for females. Alternatively, it would also be impractical for the male to care for three fledglings from a total of four. In part due to asynchronous fledging (Linkhart and McCallum 2013), which would likely result in the male caring for spatially separated fledglings and nestlings.

However, the unusual distribution of flammulated owl clutch size and a high clutch and egg mass to body mass ratio, compared with other North American Strigiformes (Linkhart, *pers. comm.*), suggest that factors other than prey provisioning may limit clutch size. Raptors with similar mean clutch sizes, including some eagles, barred owls (*Strix varia*), spotted owls (*Strix occidentalis*) and great horned owls (*Bubo virginianus*), are much larger than flammulated owls and do not frequently produce clutches larger than their mode clutch size (Gutiérrez et al. 1995; Mazur and James 2000; Buehler 2000). Clutch size distribution in these species follows a more normal distribution than in flammulated owls. This distribution may be explained by the relative investment of each egg, which is smaller compared to the adults than in flammulated owls (Gutiérrez et al. 1995, Mazur and James 2000, Buehler 2000, Linkhart and McCallum 2013). Even compared to other relatively small raptors like the boreal owl (*Aegolius funereus*), the egg mass to body mass ratio is much higher in flammulated owls (Linkhart and McCallum 2013, Haywood and Haywood 1993)

While the egg mass to body mass ratio of flammulated owls is unusual among raptors, in other avian taxa the ratio can be equally high, or higher. Kentish plovers (*Charadrius alexandrinus*), small members of the family Charadriidae, have demographic

similarities to flammulated owls despite their phylogenetic distance. Kentish plovers have an egg mass that is approximately 20% of female mass (Page et al. 2009), slightly higher than the approximately 17% in flammulated owls (Linkhart, *pers. comm.*). Additionally, like flammulated owls, Kentish plovers have a mode clutch size of three and very rarely lay larger clutches (Székely et al. 1994). Unlike raptors, Charadriidae have precocial young and provisioning young with prey is typically not thought to limit clutch size in birds with precocial young, as it does in birds with altricial young (Lack 1954). Székely et al. (1994) concluded that an inability to effectively incubate more than three eggs simultaneously limits clutch size at three in Kentish Plovers. While Kentish plovers and flammulated owls provide their young with different parental care and are phylogenetically dissimilar, they have comparable investment in egg production and likely, incubation. Flammulated owl eggs may be too large, relative to female size, for most females to adequately incubate four simultaneously. The costs of egg laying and incubation should be a focus for further research examining the limitations of flammulated owl clutch size.

Though the combination of factors limiting flammulated owl clutch size remains poorly understood, the costs of reproduction appear very high compared with other species of raptors, including boreal owls. Boreal Owls have far more variable annual reproduction than flammulated owls, with a clutch range of one to ten eggs and polygyny exhibited by some males (Korpimäki 1981, 1992). Despite rearing large broods, with almost no female contribution, mass in male boreal owls does not decline while brood rearing (Korpimäki 1990). In flammulated owls a decline of about 20% is observed in males over the course of the breeding season (Linkhart, *pers. comm.*). The relatively

large prey size of the primary prey of boreal owls in Scandinavia, voles (*Microtus* and *Clethrionomys*) (Korpimäki 1981), may allow them to raise much larger broods than flammulated owls do, despite very little female contribution to hunting. While there is little information on female mass loss in flammulated owls, the costs of reproduction are likely higher in them than in boreal owls due to a higher clutch mass to body mass ratio in flammulated owls. Despite the apparently higher costs of reproduction in flammulated owls compared to boreal owls, boreal owls have shorter lifespans (Linkhart and Reynolds 2004). The relatively long lifespan of flammulated owls is further unusual in that small size is correlated with shorter lifespan in birds (Newton 1988).

While both their lifespan and small inflexible clutch size are unusual for a bird of their size, longevity—the demographic parameter that can best explain LRS—may have been a natural evolutionary consequence of small clutch size (Newton 1989). While I have detailed other factors that may limit clutch size, the small prey size of flammulated owls likely remains an important contributing factor. Their prey base, which is likely more stable than the cyclic prey base of boreal owls (Linkhart, *pers. comm.*, Hakkarainen and Korpimäki 1994), may result in longer lifespan through facilitating recovery from reproduction.

Acknowledgements

I would like to thank Brian Linkhart whose guidance and data set made this project possible. Funding was provided through the Biology Faculty-Student Collaborative Grant, the CC Natural Sciences Divisional Grant and the Southwest Studies Jackson

Fellowship. The U.S. Forest Service and Rocky Mountain Research Station provided lodging and logistical support. Also, I would like to thank Jim Ebersole and Steven Janke for statistical assistance. Lastly, I thank Marc Snyder, Elizabeth Gustavson and Leah Lieber for suggestions and editorial support.

Works Cited

- Becker, Kirsten. "Effects of Reversed Sexual Size Dimorphism on Sex Ratio and Growth Rates of Nestling Flammulated Owls (*Otus Flammeolus*)." Thesis. *Colorado College*. 2008.
- Boyer, Alison G., Jean-Luc E. Cartron, and James H. Brown. "Interspecific pairwise relationships among body size, clutch size and latitude: deconstructing a macroecological triangle in birds." *Journal of biogeography* 37.1 (2010): 47-56.
- Buehler, David A. 2000. Bald Eagle (*Haliaeetus leucocephalus*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online:
<http://bna.birds.cornell.edu.bnaproxy.birds.cornell.edu/bna/species/506>
 doi:10.2173/bna.506
- Calder, William A. *Size, function, and life history*. Courier Dover Publications, 1996.
- Cavé, Antonius Johannes. *The breeding of the Kestrel, Falco tinnunculus L., in the reclaimed area Oostelijk Flevoland*. Vol. 18. Brill Archive, 1968.
- Charnov, Eric L., and John R. Krebs. "On clutch-size and fitness." *Ibis* 116.2 (1974): 217-219.
- Cody, Martin L. "A general theory of clutch size." *Evolution* (1966): 174-184.
- De Steven, Diane. "Clutch size, breeding success, and parental survival in the tree swallow (*Iridoprocne bicolor*)." *Evolution* (1980): 278-291.
- Eldegard, Katrine, and Geir A. Sonerud. "Sex roles during post-fledging care in birds: female Tengmalm's Owls contribute little to food provisioning." *Journal of Ornithology* 153.2 (2012): 385-398.
- Dijkstra, C., et al. "Brood size manipulations in the kestrel (*Falco tinnunculus*): effects on offspring and parent survival." *The Journal of Animal Ecology* (1990): 269-285.

- Ghalambor, Cameron K., and Thomas E. Martin. "Fecundity-survival trade-offs and parental risk-taking in birds." *Science* 292.5516 (2001): 494-497.
- Godfray, H. C. J., L. Partridge, and P. H. Harvey. "Clutch size." *Annual Review of Ecology and Systematics* 22.1 (1991): 409-429.
- Gustafsson, Lars, and William J. Sutherland. "The costs of reproduction in the collared flycatcher *Ficedula albicollis*." *Nature* 335.6193 (1988): 813-815.
- Gutiérrez, Ralph J., Alan B. Franklin, and William S. LaHaye. *Spotted Owl: Strix Occidentalis*. American Ornithologists' Union, 1995.
- Hanssen, Sveinn Are, et al. "Cost of reproduction in a long-lived bird: incubation effort reduces immune function and future reproduction." *Proceedings of the Royal Society B: Biological Sciences* 272.1567 (2005): 1039-1046.
- Hakkarainen, Harri, and Erkki Korpimäki. "Does feeding effort of Tengmalm's owls reflect offspring survival prospects in cyclic food conditions?." *Oecologia* 97.2 (1994): 209-214.
- Hayward, G. D. and P. H. Hayward. 1993. Boreal Owl (*Aegolius funereus*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: <http://bna.birds.cornell.edu.bnaproxy.birds.cornell.edu/bna/species/063> doi:10.2173/bna.63
- Holthuijzen, Anthonie MA. "Prey delivery, caching, and retrieval rates in nesting Prairie Falcons." *Condor* (1990): 475-484.
- Jones, Isabel. "The effects of gender and brood size on the development of Flammulated Owl (*Otus flammeolus*) nestlings." Thesis. *Colorado College*. 2012.
- Korpimäki, Erkki. "On the ecology and biology of Tengmalm's Owl (*Aegolius funereus*) in southern Ostrobothnia and Suomenselka, western Finland." *Acta University Ouluensis A 118 Biology* (1981):1-84.
- Korpimäki, Erkki. "Clutch size, breeding success and brood size experiments in Tengmalm's owl *Aegolius funereus*: a test of hypotheses." *Ornis Scandinavica* (1987): 277-284.
- Korpimäki, Erkki. "Costs of reproduction and success of manipulated broods under varying food conditions in Tengmalm's owl." *The Journal of Animal Ecology* (1988): 1027-1039.
- Korpimäki, Erkki. "Body mass of breeding Tengmalm's Owls *Aegolius funereus*: seasonal, between-year, site and age-related variation." *Ornis Scandinavica* (1990): 169-178.
- Korpimäki, Erkki. "Fluctuating food abundance determines the lifetime reproductive success of male Tengmalm's owls." *Journal of Animal Ecology* (1992): 103-111.

- Lack, David. "The significance of clutch-size." *Ibis* 89.2 (1947): 302-352.
- Lack, David. "The natural regulation of animal numbers." *The Natural Regulation of Animal Numbers*. (1954).
- Leckie, Fiona M., et al. "Parental differences in brood provisioning by Hen Harriers *Circus cyaneus*: Capsule Females varied their provisioning patterns according to brood age and brood size, whereas males did not." *Bird Study* 55.2 (2008): 209-215.
- Lindén, Mats, and Anders Pape Møller. "Cost of reproduction and covariation of life history traits in birds." *Trends in Ecology & Evolution* 4.12 (1989): 367-371.
- Linkhart, Brian D. and D. Archibald McCallum. 2013. Flammulated Owl (*Psiloscops flammeolus*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: <http://bna.birds.cornell.edu.bnaproxy.birds.cornell.edu/bna/species/093>
doi:10.2173/bna.93
- Linkhart, Brian D., and Richard T. Reynolds. "Brood division and postnesting behavior of Flammulated Owls." *The Wilson Bulletin* (1987): 240-243.
- Linkhart, Brian D., and Richard T. Reynolds. "Longevity of Flammulated Owls: additional records and comparisons to other North American strigiforms." *Journal of Field Ornithology* 75.2 (2004): 192-195.
- Linkhart, Brian D., and Richard T. Reynolds. "Return rate, fidelity, and dispersal in a breeding population of flammulated owls (*Otus flammeolus*)." *The Auk* 124.1 (2007): 264-275.
- Linkhart, Brian D., Richard T. Reynolds, and Ronald A. Ryder. "Home range and habitat of breeding Flammulated Owls in Colorado." *The Wilson Bulletin* (1998): 342-351.
- Löhrl, Hans. "Einfluss der brutraumfläche auf die geleggrösse der kohlmeise (*Parus major*)." *Journal of Ornithology* 114 (1973): 339-347.
- Masman, Dirkjan, et al. "Energetic limitation of avian parental effort: field experiments in the kestrel (*Falco tinnunculus*)." *Journal of Evolutionary Biology* 2.6 (1989): 435-455.
- Mazur, Kurt M. and Paul C. James. 2000. Barred Owl (*Strix varia*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: <http://bna.birds.cornell.edu.bnaproxy.birds.cornell.edu/bna/species/508>
doi:10.2173/bna.508

- Meijer, Theo, Serge Daan, and Michael Hall. "Family planning in the kestrel (*Falco tinnunculus*): the proximate control of covariation of laying date and clutch size." *Behaviour* (1990): 117-136.
- Monaghan, Pat, and Ruedi G. Nager. "Why don't birds lay more eggs?." *Trends in Ecology & Evolution* 12.7 (1997): 270-274.
- Murray, Gale A. "Geographic variation in the clutch sizes of seven owl species." *The Auk* (1976): 602-613.
- Newton, Ian. *The Sparrowhawk*. T&AD Poyser, Staffordshire, 1986.
- Newton, Ian. "Population Ecology of Raptors." Berkhamsted: Poyser, 1989.
- Newton, Ian. *Population limitation in birds*. Academic press, 1998.
- Nur, Nadav. "The consequences of brood size for breeding blue tits I. Adult survival, weight change and the cost of reproduction." *The Journal of Animal Ecology* (1984): 479-496.
- Olsen, Penny, Veronique Doyle, and Mark Boulet. "Variation in male provisioning in relation to brood size of Peregrine Falcons *Falco peregrinus*." *Emu* 98.4 (1998): 297-304.
- Page, Gary W., Lynne E. Stenzel, G. W. Page, J. S. Warriner, J. C. Warriner and P. W. Paton. 2009. Snowy Plover (*Charadrius nivosus*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online:
<http://bna.birds.cornell.edu.bnaproxy.birds.cornell.edu/bna/species/154>
doi:10.2173/bna.154
- Perrins, C. M. "Population fluctuations and clutch-size in the Great Tit, *Parus major* L." *The Journal of Animal Ecology* (1965): 601-647.
- Perrins, C. M., and D. Moss. "Reproductive rates in the great tit." *The Journal of Animal Ecology* (1975): 695-706.
- Reynolds, Richard T., and Brian D. Linkhart. "Methods and materials for capturing and monitoring Flammulated Owls." *Western North American Naturalist* 44.1 (1984): 49-51.
- Reynolds, Richard T., and Brian D. Linkhart. "The nesting biology of Flammulated Owls in Colorado." *Biology and conservation of northern forest owls*. RW Nero, RJ Clark, RJ Knapton, and RH Hamre, editors. USDA Forest Service General Technical Report RM-142 (1987): 239-248.
- Skutch, Alexander F. "Do tropical birds rear as many young as they can nourish." *Ibis* 91.3 (1949): 430-458.

- Slagsvold, Tore. "Clutch size variation in passerine birds: the nest predation hypothesis." *Oecologia* 54.2 (1982): 159-169.
- Sonerud, Geir A. "Functional responses of birds of prey: biases due to the load-size effect in central place foragers." *Oikos* (1992): 223-232.
- Styrsky, Jennifer Nesbitt, Jeffrey D. Brawn, and Scott K. Robinson. "Juvenile mortality increases with clutch size in a neotropical bird." *Ecology* 86.12 (2005): 3238-3244.
- Székely, T., I. Karsai, and T. D. Williams. "Determination of clutch-size in the Kentish Plover *Charadrius alexandrinus*." *Ibis* 136.3 (1994): 341-348.
- Thompson, Bruce C., et al. "Nest success is not an adequate comparative estimate of avian reproduction." *Journal of Field Ornithology* 72.4 (2001): 527-536.
- Tinbergen, Joost M., and Juan J. Sanz. "Strong evidence for selection for larger brood size in a great tit population." *Behavioral Ecology* 15.4 (2004): 525-533.
- Tolonen, Pasi, and Erkki Korpimäki. "Determinants of parental effort: a behavioural study in the Eurasian kestrel, *Falco tinnunculus*." *Behavioral Ecology and Sociobiology* 35.5 (1994): 355-362.
- Van Noordwijk, A. J., JH van Van Balen, and W. Scharloo. "Genetic and environmental variation in clutch size of the great tit (*Parus major*)." *Netherlands Journal of Zoology* 31.2 (1980): 342-372.
- Visser, M. E., and C. M. Lessells. "The costs of egg production and incubation in great tits (*Parus major*)." *Proceedings of the Royal Society of London. Series B: Biological Sciences* 268.1473 (2001): 1271-1277.
- Wiebe, Karen L., and Trisha L. Swift. "Clutch size relative to tree cavity size in Northern Flickers." *Journal of Avian Biology* 32.2 (2001): 167-173.
- Williams, George C. "Natural selection, the costs of reproduction, and a refinement of Lack's principle." *American naturalist* (1966): 687-690.

Table 1. Total sampling effort, which included laying, incubation, nestling and post-fledging periods.

	Totals			Nestling Period				Incubation Period	
	Observation Time (hours)	Nests (#)	Prey Deliveries (#)	Prey Deliveries (#)	Observation Time (hours)	Male Prey Deliveries (#)	Female Prey Deliveries (#)	Prey Deliveries (#)	Observation Time (hours)
All Nests	302	156	3556	2853	185.5	1594	556	207	59.75
Broods of 2	118.5	60	1213	1049	78.25	754	188	68	31.25
Broods of 3	134.25	59	2064	1620	93.5	732	334	97	18.25

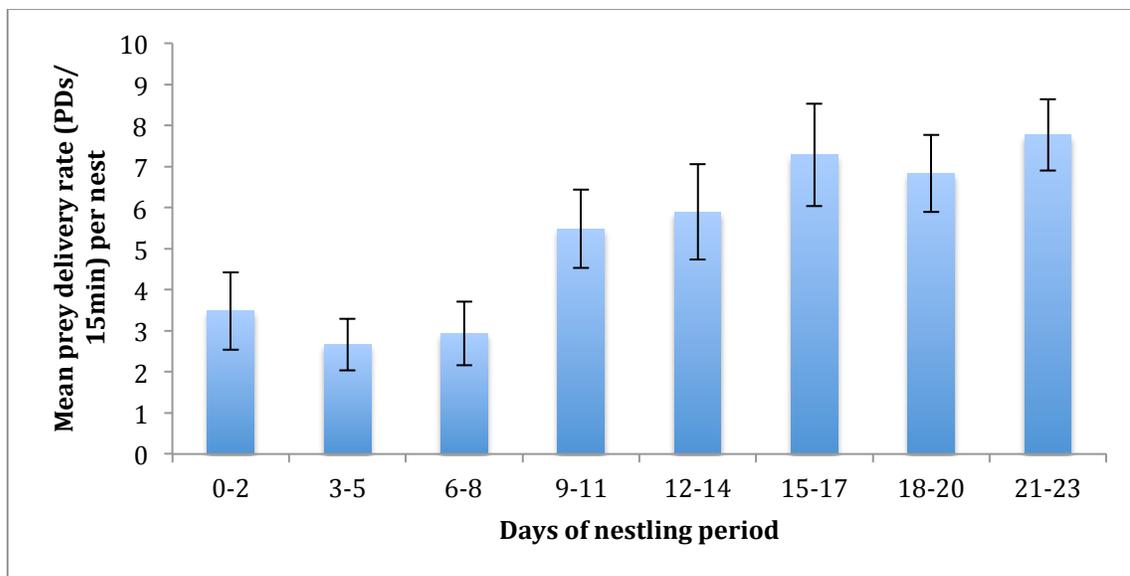


Figure 1. Mean prey delivery rate during the first hour of activity throughout the nestling period. Error bars represent standard error.

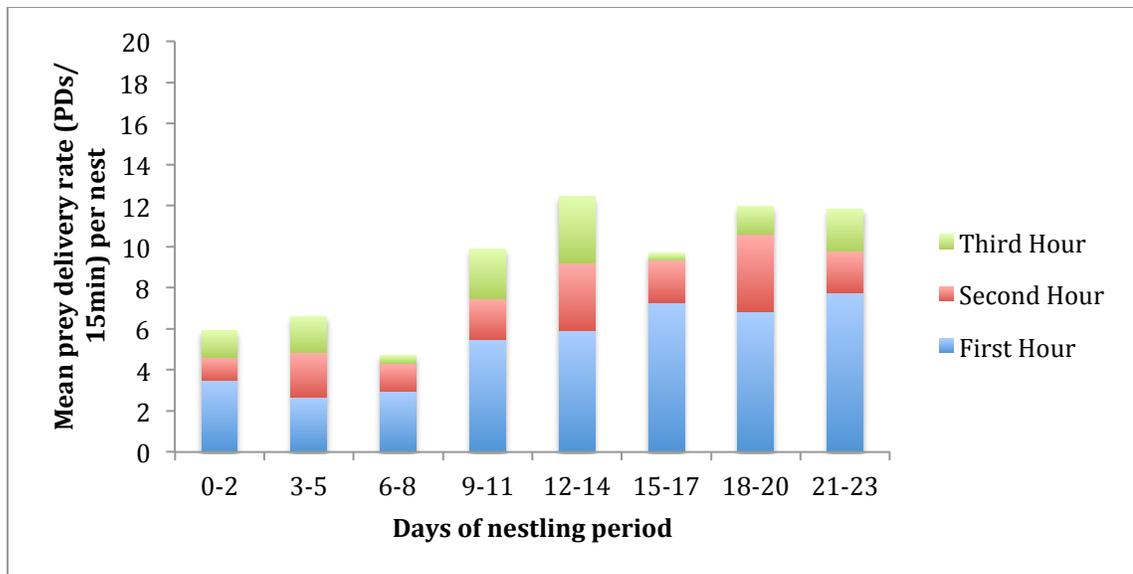


Figure 2. Mean prey delivery rate during the first, second and third hours of activity, throughout the nestling period.

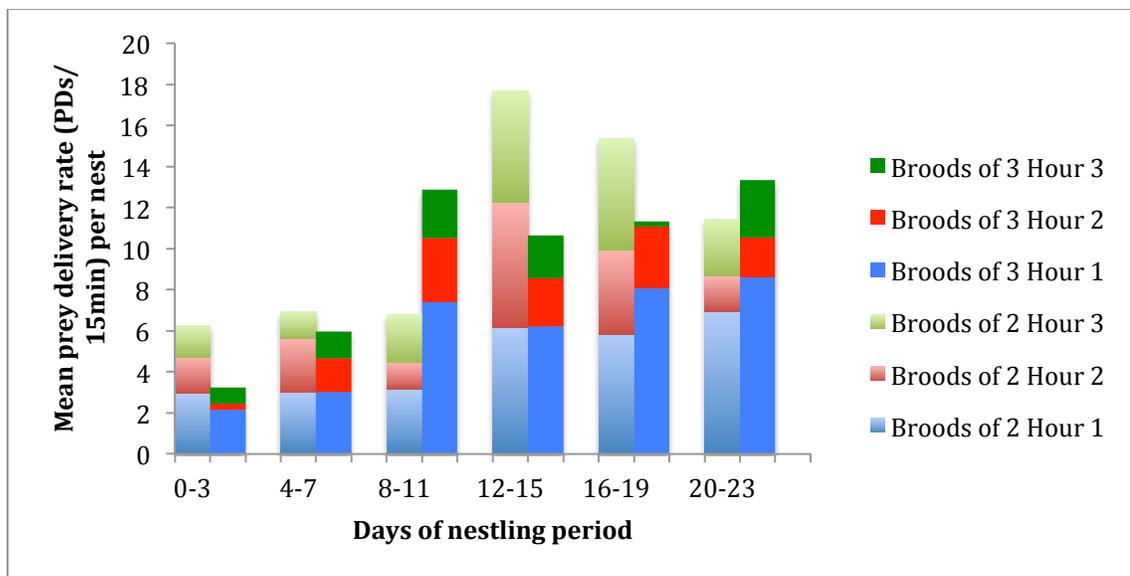


Figure 3. Mean prey delivery rate during the first, second and third hours of activity. Nests are separated by brood size.

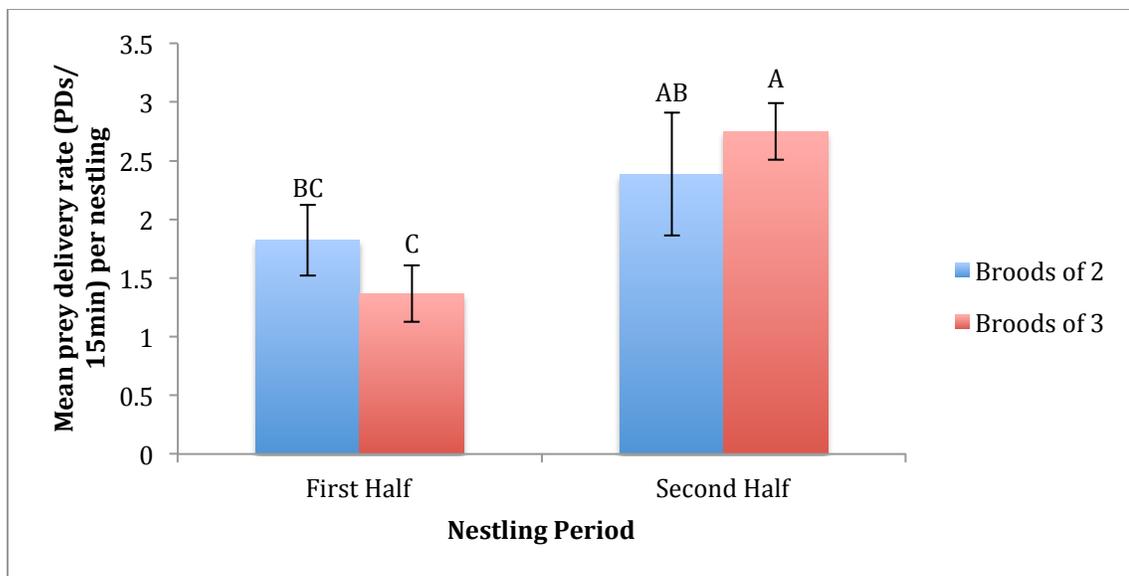


Figure 4. Mean prey delivery rate per nestling in broods of two vs. broods of three during the first hour of activity during the first and second half of the nestling period. Error bars represent SE. Letters indicate the results of one-way ANOVA and Tukey-Kramer test.

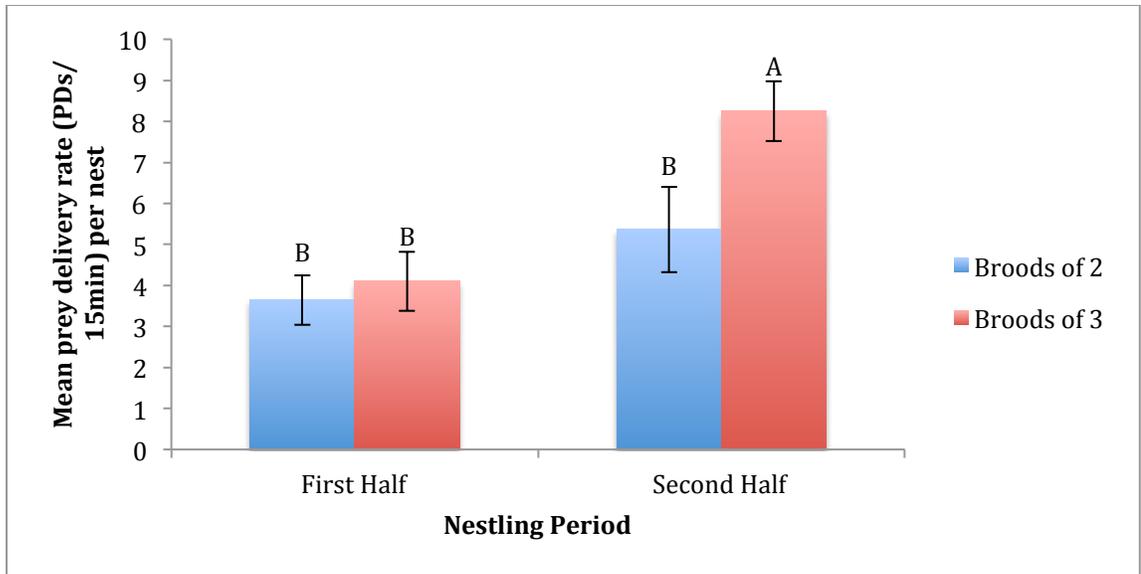


Figure 5. Mean prey delivery rate observed per nest in broods of two vs. broods of three during the first hour of activity during the first and second half of the nestling period. Error bars represent SE. Letters indicate the results of one-way ANOVA and Tukey-Kramer test.

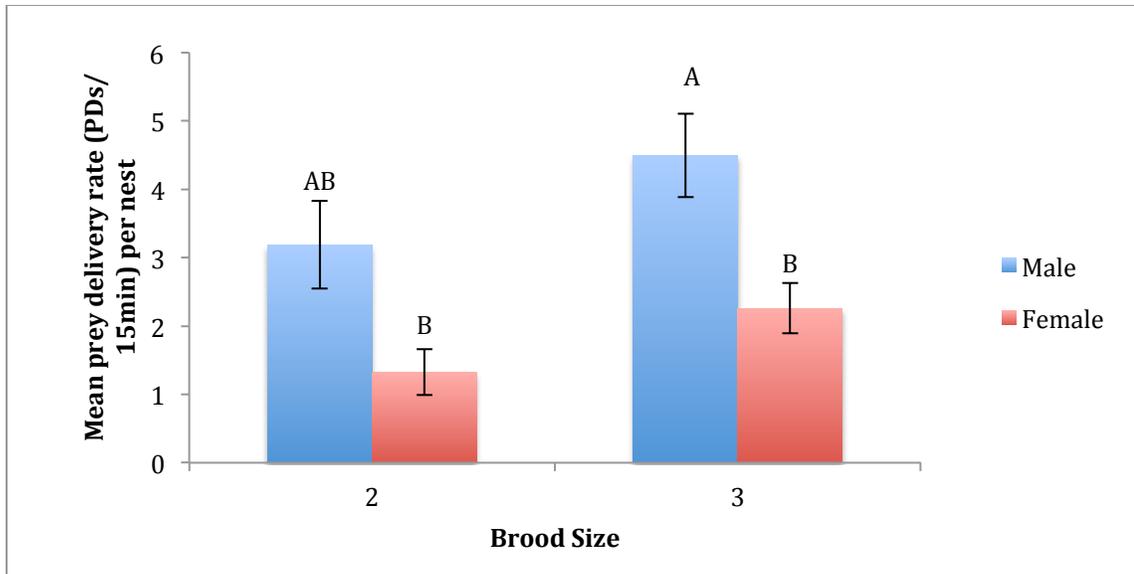


Figure 6. Mean rate of prey deliveries by male and female parents with broods of two vs. broods of three during the first hour of activity and the last twelve days of the nestling period. Error bars represent SE. Letters indicate the results of one-way ANOVA and Tukey-Kramer test.

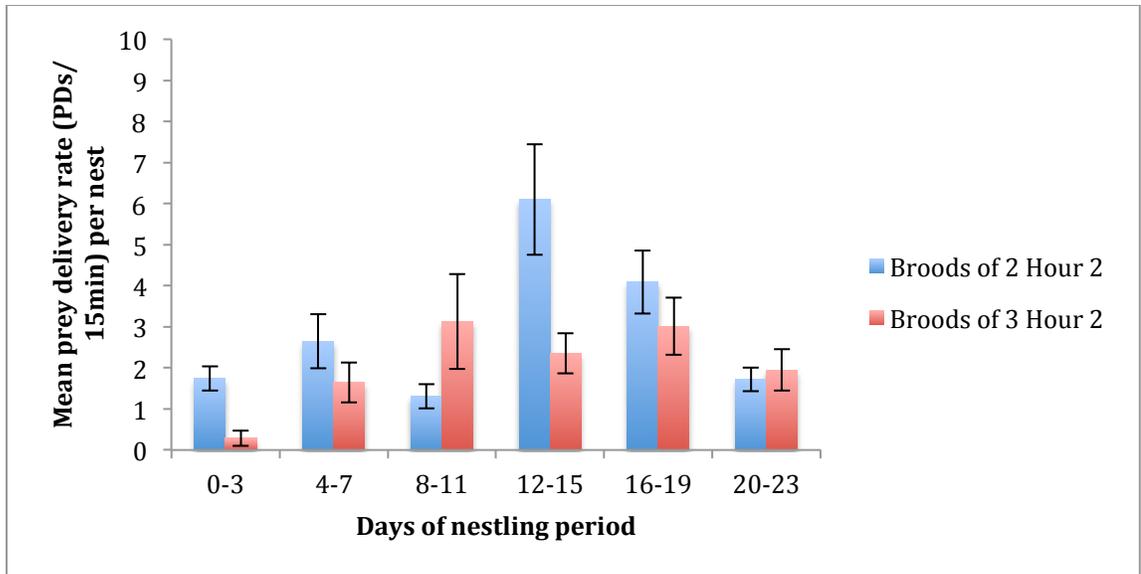


Figure 7. Mean prey delivery rate during the second hour of activity in broods of two vs. broods of three. Error bars represent standard error.

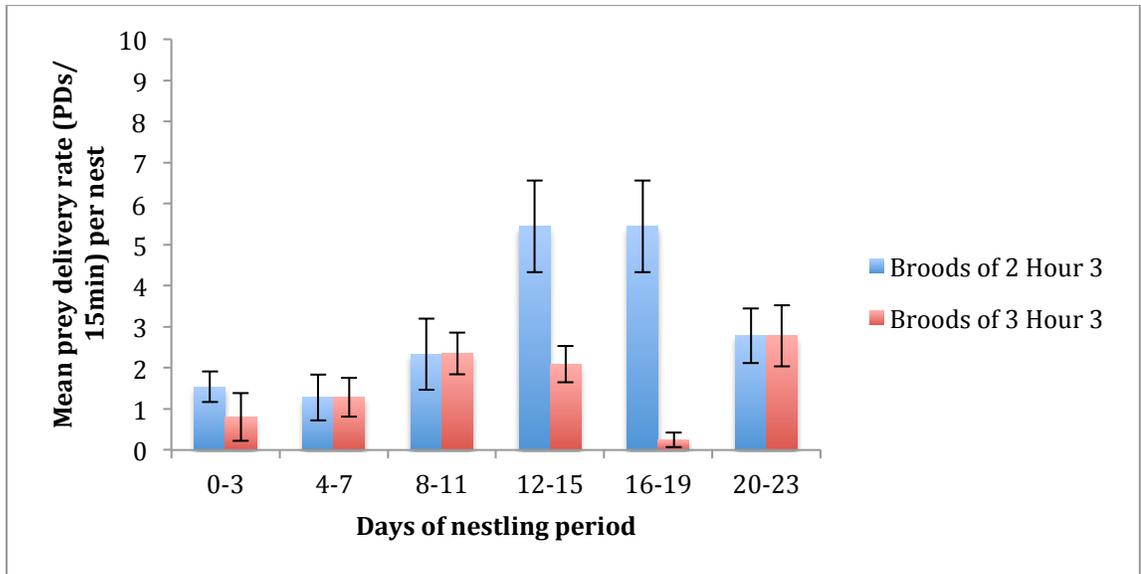


Figure 8. Mean prey delivery rate during the third hour of activity in broods of two vs. broods of three. Error bars represent standard error.