Individual Variation in Foraging Effort of Breeding Birds

by

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B.A., Connecticut College, 2013

Thesis Submitted in Partial Fulfillment of the
Requirements for the Degree of
Master of Science

in the
Department of Biological Sciences
Faculty of Science

SIMON FRASER UNIVERSITY

Summer 2017

Approval

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Abstract

Parental care (e.g. provisioning nestlings) is widely assumed to be costly, and life-history theory predicts a trade-off between reproduction and future fecundity and/or survival. However, experimental studies manipulating workload during parental care and demonstrating fitness effects are either rare or have mixed results. Here, we took a two-step approach to this problem in European starlings (Sturnus vulgaris): 1) using a 4-year dataset to ask if changes in parental investment in handicapped (wing-clipped) parents, and the fitness consequences of these decisions, vary among years (i.e. with ecological context), and 2) using an automated radio telemetry system to determine if females alter their activity to compensate for an increase in workload. We found marked individual and annual variation in response to the handicapping treatment. In addition, clipped individuals dramatically reduced their activity, while sustaining current breeding productivity, suggesting that clipped individuals reduce self-maintenance to favour their current reproductive bout.

Keywords: Parental investment; wing-clipping; automated radio telemetry; activity; life-history theory

Acknowledgements

I want to first thank my Senior Supervisor, Dr. Tony Williams, for his unwavering support and direction. Tony always had his door open, left no email unanswered, and spent many hours and hard work in the field with me. I owe my development as a researcher and biologist to him. I would also like to thank Dr. David Green and Dr. Ronald Ydenberg for their helpful feedback and guidance as members of my supervisory committee.

This research would not have been possible without the amazing generosity of the Davis family. They kindly let me, and even helped me, build massive radio towers on their property. I will miss working with such a friendly and accommodating family.

I am endlessly grateful to the Williams Lab, specifically Allison Cornell and Jeff Yap. They have been an extremely supportive group, and I have truly enjoyed my time with them whether it be discussing R code or chatting over beer and nachos.

This work was funded by The Natural Sciences and Engineering Council of Canada's Discovery, Accelerator, and Research Tools and Equipment Category 1 Grants to Dr. Tony D. Williams (Grant numbers, 155395-2012-RGPIN, RGPAS/429387-2012, EQPEQ 458525-2014).

Lastly, I would like to thank my family and friends for their love and support. Thanks to my family for always supporting my decisions. The friends I have made since moving to Vancouver are some of the warmest and funniest people, and they have made my time here very meaningful. I especially want to thank Stephanie Seidmon for being the absolute best!

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Chapter 1.

General Introduction

Free-living animals show marked variation in the amount of parental care, broadly defined as anything parents do that increases the growth and/or survival of their offspring. For example, in mammals, only 5-10% of species have bi-parental care and males mainly invest in reproduction through efforts to enhance reproductive success, (e.g., courtship displays, intrasexual combat). In contrast, paternal care is most common in fish (> 50% of species) whereas in birds bi-parental care occurs in 90% of species, with males feeding chicks and sometimes incubating eggs. There is also marked variation in how reproductive investment is partitioned among one or more reproductive bouts. For example, some individuals invest all of their resources into one reproductive bout, while other individuals are more likely to desert their nest when facing an imminent threat. As extreme examples, Penduline tits, *Remiz pendulinus*, desert their nests 30-40% of the time (Szentirmai et al. 2007), whereas male Australian redback spiders, *Latrodectus hasselti,* activiely assist the female in sexual cannibalism (letting themselves be eaten) to increase their fitness for that one reproductive bout (Andrade, 1996).

Not only does parental care vary between species, but also between individuals in a given species (Nakagawa et al. 2007; Westneat et al. 2011; Williams, 2012). For many birds, energy expenditure peaks during the chick-rearing period, and parents make a series of decisions during this period with direct consequences for reproduction (Bryant and Westerterp, 1980; Drent and Daan, 1980). One dominant model of reproductive decisions is central place foraging, which predicts that individuals will maximize net energetic gain each foraging trip (Kacelnik 1984; Stephens et al. 2007; Tinbergen, 1981) by selecting the most energetically profitable foraging patches (closest and most profitable resources) and the most energetically profitable prey items (Stephens et al. 2007; Ydenberg and Davies, 2010). Time spent foraging is optimized based on the profitability of the given patch. In addition, a chick-rearing bird must collect prey items for both delivery and consumption. Therefore, there is a trade-off between energy spent on provisioning chicks and self-feeding.

Trade-offs are ubiquitous in biology and represent a guiding principle in life-history theory (Stearns, 1989). Perhaps the most widely accepted trade-off in life-history theory is the cost of reproduction: the idea that individuals must balance their reproductive success in one year with survival and subsequent fecundity (Clutton-Brock et al. 1983; Tavecchia et al. 2005). Costs of reproduction are thought to be widespread and have been studied in fish (Lester et al. 2004), insects (Lee et al. 2008), reptiles (Olsson et al. 1997), and birds (Gustafsson et al. 1994). More specifically, in birds, life-history theory predicts that individuals that invest more resources into parental care will fledge more and better quality offspring, but will suffer a cost in terms of reduced survival and future fecundity. Remarkably, evidence supporting this trade-off, particularly in female birds, is mixed (reviewed in Santos and Nakagawa 2012). Provisioning rate, or the number of times a parent brings food to the nest in a given time period, is the most commonly used metric to quantify parental workload (Bowers et al. 2014; Gray et al. 2005; García-Navas and Sanz 2011; Nur 1984; Stephens et al. 2007). Furthermore, many studies have found marked interindividual variation in provisioning rate, and yet no relationship between provisioning rate and the number of chicks fledged and chick quality (Dawson and Bortolotti 2003; Mariette et al. 2011; Schwagmeyer and Mock 2008). However, birds can vary workload by altering their foraging behaviour (i.e. load size, prey type, foraging distance) (Mariette et al. 2011; Paredes et al. 2005; Weimerskirch et al. 1995; Wright et al. 1998).

In general, it is more difficult to collect large amounts of data on metrics of parental care, such as foraging effort (load size, prey type, foraging distance), compared with data on timing of egg-laying or number of eggs (Williams 2012). Nevertheless, new advances in technological methods for wildlife tracking and bio-logging are giving biologists an unparalleled ability to track free-living animals (Wilmers et al. 2015). Animal borne sensors and nest cameras now allow researchers to measure more dynamic aspects of foraging behaviour that were previously challenging to measure or that required direct observation. For example, radio collars equipped with GPS and accelerometers measured the energetic expenditure of differing foraging strategies in Pumas, *Puma concolor* (Williams et al. 2014). Automated radio telemetry allows for the collection of large amounts of data over a relatively long period of time, and has recently been used in a variety of ecological studies (Adelman et al. 2010; Steiger et al. 2013; Ward et al. 2014). Nonetheless, this technology has yet to be applied to understanding parental workload.

In this thesis, I investigate reproductive decisions of individual female European starlings, *Sturnus vulgaris*, when subject to an experimentally increased workload (i.e. wing-clipping and/or weight from a radio transmitter). The European starling is a fantastic study species for understanding parental workload. Foraging behaviour and decisions in European starlings is well documented, since they readily breed in nest boxes and forage in open pastures (Kacelnik 1984; Tinbergen, 1981; Westerterp, 1973; Wright et al. 1998). In addition, nestling starling diet is known to primarily consist of tipulid larvae (Dunnet 1955; Tinbergen, 1981). Therefore, we can exploit the advantages of a well-known system by introducing automated radio tracking and nest box cameras in order to get an unprecedented look at parental workload and the mechanistic drivers behind the trade-off of reproduction and survival.

In chapter 1, I use a four-year dataset to look at the effects of an increased workload across years of different, known ecological contexts. The main question here is whether clipped individuals alter their current reproductive investment, current productivity, or future productivity depending on the ‘quality’ of the year when birds were manipulated. In chapter 2, I analyze data from an automated radio telemetry system to determine activity of handicapped individual starlings (i.e. behavioural responses to handicapping) from late incubation through the entire-chick-rearing period. We combined radio tracking with a) video analysis of prey brought back to the nest, and b) a handicapping experiment (wing-clipping) to investigate changes in foraging behaviour in response to experimentally-increased workload. We tested whether the clipped individuals mediate the effect of their handicap by looking at a variety of foraging behaviour metrics (i.e. provisioning rate, prey type, number of prey, and activity).

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Chapter 2.

Context-dependency of effects of manipulated workload during parental care on costs of reproduction

2.1. Introduction

Reproduction is widely assumed to be costly, particularly when it entails extensive parental care. Life-history theory predicts that individuals that invest more in parental care should benefit in terms of number of offspring produced, but that increased parental care might come at a cost in terms of decreased future fecundity and/or survival (Stearns, 1992). A seemingly straightforward question, the cost of reproduction has puzzled researchers for decades (Harshman and Zera, 2007). However, there remains only equivocal evidence to support a trade-off between parental care and survival in birds, especially for females (Mitchell et al., 2012; Santos and Nakagawa, 2012). Furthermore, the notion that parents who work "harder" (commonly measured by the rate at which parents provision their chicks) produce more, better quality chicks is surprisingly poorly supported (Schwagmeyer and Mock, 2008; Williams, 2012).

Two key problems in studying costs of parental care are 1) that it might be unusual for free-living animals to operate at, or close to, their maximum performance capacity (the idea of "ecological performance," Irschick and Garland (2001), Irschick and Higham (2016)), and 2) that any costs of parental care should be context dependent, mainly being expressed in poor, low resource years. Understanding these costs requires experimental manipulation of workload during parental care, knowledge of ecological context when experimental manipulations are conducted, and preferably, that experiments be conducted over multiple years (where ecological context will likely vary). The cost of reproduction associated with parental care has been studied extensively in birds, but most studies to date, including all studies used in Santos and Nakagawa's (2012) meta-analysis, use brood size manipulations as a means to increase workload (Williams, 2012). More often than not in these studies, total provisioning rate per nest increases, but average provisioning rate per chick decreases. Individuals are thus able to raise more offspring, albeit of poorer quality (reviewed in Williams, 2012). Piersma (2011) suggests that animals, when challenged, (i.e. brood size increase) are simply not able to work harder; however, individuals may be choosing not to work harder (reviewed in Fowler and Williams, 2015). Whereas a direct manipulation (i.e. wing-clipping or the addition of the weight) results in an unavoidable biochemical effect, and the individual will suffer costs by maintaining and increasing workload. In addition, manipulation may directly affect the nestlings, leading to reduced quality or increased mortality (e.g. Velando and Alonso-Alvarez, 2003; Sæther et al., 1993). Parents, on the other hand, may incur immediate costs (Weimerskirch et al. 1995), or costs may develop more slowly and only become evident after the breeding season (Winkler and Allen, 1995). Moreover, other methods for direct manipulation of workload (e.g. wing-clipping, adding weights) results in an unavoidable increase in the cost of flight during parental care, and should therefore be more likely to reveal costs of reproduction. Nevertheless, wing-clipping experiments have also produced mixed, contradictory, and equivocal results. Handicapped birds may reduce their provisioning rate and lower their productivity (Jacobs et al., 2013; Slagsvold and Lifjeld, 1988) but have similar return rates as unmanipulated individuals (Bijleveld and Mullers, 2009; Wright and Cuthill, 1989). In contrast, other studies have found that clipped birds have lower returns rates (Winkler and Allen, 1995) or lower current productivity (Love and Williams, 2008). Additionally, the vast majority of wing-clipping studies have been conducted in a single year (Bijleveld and Mullers, 2009; Harding et al., 2009; Jacobs et al., 2013; Navarro and González-Solís, 2006; Sanz et al., 2000; Slagsvold and Lifjeld, 1988; Tieleman et al., 2008; Wegmann et al., 2015; Weimerskirch et al. 1995). Furthermore, few wing-clipping studies go beyond return rate as a measure of survival and fail to record differences in future productivity (but see, Hegemann et al., 2013) Therefore, the mixed results of these studies could be due to the lack of variation in ecological context and/or the metrics used to quantify workload. For example, barn swallows work harder (i.e. have higher daily energy expenditure) when the foraging conditions are favourable (Schifferli et al., 2014). Thus, the short term nature of most experimental studies to date makes it impossible to place their results into ecological context (i.e. whether the year was a relatively ‘good’ or ‘bad’ year compared to other years).

Here, we use a 4-year dataset to analyze reproductive decisions of individual female European starlings when subject to an experimentally increased workload (i.e. wing-clipping and/or added weight from a radio transmitter). Using a gradient of experimental manipulation (control female, radio-tagged female, and additive effect of wing-clipping and radio tagged female) across years of different, known ecological contexts, we were able to investigate the effects of increased workload on current reproductive investment (abandonment, mass loss, provisioning rate), current reproductive productivity (number and size of offspring), and future fecundity and survival (second brood size at fledge, cumulative breeding output over a two-year period, and local return rate). First, we predicted that individuals trade off their current investment and productivity for future productivity. Secondly, we predicted that these decisions are based on the ecological context of the year, so that individuals in ‘good’ years are more likely to sacrifice their body condition to increase productivity and offspring quality.

2.2. Methods

2.2.1. Breeding data

Data was collected from a long-term study (data presented here is from 2013 to 2016) of a nest-box colony of European starlings at Davistead Dairy Farm, Langley, British Columbia, Canada (49 ° 81’0N, 122 ° 85’0W). The field site houses approximately 80 breeding pairs each year, using nest boxes mounted on the buildings, fences, and posts. Each year we followed the same protocol: we checked nest boxes daily starting at the end of March to record laying date, clutch size, brood size at hatch, and brood size at fledging. When the chicks were 17 days old (shortly prior to fledging), we measured chick size (i.e. fledgling mass, tarsus length, and wing chord length). During mid-incubation, we captured individually breeding females and fitted them with color bands and individually numbered metal bands (Environment Canada # 10646). We did not band males, therefore their identity is unknown. We repeated this process for second broods, beginning ~31 days (10 days of incubation, 21 days to fledging) after clutch completion of the earliest first clutch. Any female who laid an egg during this time period was said to have initiated a second brood. Individuals were assigned to three treatment groups, control females (ctrl), control females with radio transmitters (ctrlRT), and clipped females with radio transmitters (clipRT). There was no significant difference in the lay date ($F_{2,188} = 0.72$, $P = 0.49$), clutch size ($F_{2,188} = 0.47$, $P = 0.63$), or body mass ($F_{2,188} = 1.45$, $P = 0.24$) of the individual females subsequently assigned to each of the treatment groups. Females were fitted with a digitally coded radio transmitters (Lotek Wireless Inc) by means of a leg loop harness (2013: n = 19; 2014: n = 32; 2015: n = 30; 2016: n = 43) (Rappole and Tipton, 1991). The weight of the transmitters (≤ 2.1g) is less than the suggested 5% of the body weight threshold given the average mass of female European starlings during these years was 82.9g (Naef-Daenzer 1993). Nevertheless, we consider females with radio transmitters a separate treatment given that other studies have found transmitter effects (Godfrey et al., 2003; Pennycuick et al., 1990).

2.2.2. Wing clipping

Females were clipped in years 2014 (n = 16), 2015 (n = 15), and 2016 (n = 21). Birds assigned to the clipRT treatment had every third primary feather (i.e. primaries 3, 6, and 9) from each wing removed near its base with scissors. We estimated average wing surface area, from wing photos, for both wings = 142 cm^2 and mean body mass = 82.9 g, so wing loading in non-manipulated adults = 82.9 g/142 cm^2 = 0.583 g/cm^2. Adding a 2 g radio-transmitter with no change in body mass increases an estimated wing loading to 0.597 g/cm^2 (+ 2.4%). However, birds lost 3.3 g on average by the chick-rearing stage so wing loading would actually be lower (-3.7%). Calculating the effect of wing-clipping is more complicated: when wings were held in a natural, relaxed position, gaps between feathers due to removal of primaries 3, 6, and 9 were not evident because adjacent feathers overlapped; estimated surface area for outlined wings was only -0.8% lower in clipped birds ($P > 0.05$). If we stretched wings out so that gaps were accentuated and drew an outline around the gaps, wing area was, on average, 17.7% lower after clipping. This would result in estimated wing-loading = 0.696 before mass loss (+19.3%), and 0.675 after mass loss (+ 15.8%). This therefore represents a maximum magnitude of effect, but likely one that is biologically unrealistic since it ignores any behavioural adjustments birds can make (changes to wing angle, feather orientation), which would affect the aerodynamic properties during actual flight to compensate for lost feathers. Nevertheless, clipped birds would clearly be more aerodynamically challenged, with increased wing-loading, than non-clipped birds, increasing costs of foraging flights. The effect of this treatment is temporary, as individuals replace these feathers during the post-breeding moult. On day 10 post-hatching, females were re-captured and weighed again (except for 2015).

2.2.3. Provisioning data

We assessed parental provisioning rate on days 6, 7, and 8 post-hatching, either 3 times (84%) or twice (16%) over the three days. All observations were conducted over a period of 30 minutes between 09:00 and 14:00. We standardized the timing of observations so that individuals were not sampled at the same time each day. We chose days 6-8 since they represent the period of most rapid chick growth, and here we use the mean nest visitation rate over the 3 days. A detailed analysis by Fowler and Williams (2015) from this same field site found that nest visitation rate was highly correlated among successive days. Therefore, nest visitation rate is repeatable and justifies our use of the mean.

2.2.4. Statistical analysis

Here, we restricted our analysis to individuals who were only assigned to a treatment group in one of the years (i.e. ctrlRT or clipRT), excluding 22 individuals from the analysis. All analyses were completed in R STUDIO version 0.98.1028 (R Studio Team 2015) using lsmeans (Lenth 2016), lme4 (Bates et al. 2014), lmtest (Zeileis and Hothorn 2002), nlme (Pinheiro et al. 2013), stats (R Studio Team 2015), and multcomp (Hothorn et al. 2008). We used a linear-mixed effects modeling approach to test whether individuals within the three treatment groups vary in current reproductive investment, current reproductive productivity, and future fecundity. We used individual (band number) as a random factor. Analyses for mass loss were restricted to years 2013, 2014, and 2016, as we did not recapture females while chick-rearing in 2015. Moreover, not all individuals were recaptured every year (total recaptured = 86). Analysis for cumulative brood size at fledge (the number of chicks fledged from the individual's first brood) was restricted to individuals that were first captured in 2013, 2014, and 2015 since local return rate for individuals captured in 2016 is not yet known. We used a chi-square analysis for analysis of abandonment, second brood initiation, and local return rate. For all analyses (excluding abandonment analysis) we removed individuals who abandoned immediately following capture during incubation. However, given that some individuals that abandoned returned the following year we included them in future productivity analyses. To deal with the unbalanced nature of this study (only ctrl and ctrlRT females in 2013; whereas, in 2014, 2015, and 2016 we included an additive clipRT treatment), we took a stepwise approach to our analysis. We first analyzed ctrl females and ctrlRT females across all four years (model 1) to test for an effect of radio-transmitter attachment only, and then we analyzed all three treatment groups for years 2014-16 to test for an additive effect of wing-clipping (model 2). Year quality was determined by comparing the productivity of the control groups each year. Finally, we used mixed models to compare variation in productivity by year. We again used individual (band number) as a random factor. Significance was determined using a likelihood ratio test against a null model.

2.3. Results

2.3.1. Assessing year quality using control females

On average control females raised 3.46 ± 1.97 chicks from their first brood across all four years (excluding abandoned nests). Brood size at fledge varied for ctrl females over the course of the four year study period ($\chi^2_{[3]} = 13.73$, $P < 0.01$; Table 2.1). We therefore use brood size at fledge for control females as one measure to determine year ‘quality’. Productivity was highest in 2015 (4.58 ± 1.2 chicks, a “good” year), lowest in 2013 (2.70 ± 2.1 chicks, a “bad” year) and intermediate in 2014 (3.06 ± 1.9 chicks) and 2016 (3.76 ± 1.2 chicks; latter values were not significantly different from other years; $P > 0.05$ in all cases). Fledgling mass also varied among years ($\chi^2_{[3]} = 26.86$, $P < 0.0001$). Fledgling mass was significantly higher in 2016 (80.2 g ± 2.6) than all other years ($P < 0.05$ in all cases) with no difference between 2013, 2014 or 2015 ($P > 0.05$ in all cases; Table 2.1). Fledgling tarsus varied across years ($\chi^2_{[3]} = 18.53$, $P < 0.001$) and was lower in 2014 than all other years ($P < 0.01$ in all cases) with no differences among other years ($P > 0.05$ in all cases; Table 2.1). Finally, fledgling wing chord varied across years ($\chi^2_{[3]} = 38.69$, $P < 0.001$) and was greater in 2016 compared with all other years ($P < 0.01$ in all cases) with no difference among other years ($P > 0.05$ in all cases; Table 2.1). Based on these data we categorized years as follows: a) 2013 = a "bad" year (very low BSF); b) 2014 = "intermediate" to "poor" year (average BSF but lowest mean tarsus at fledging); c) 2015 = "good" year (highest BSF); and d) 2016 a "good" year (above average BSF, highest chick fledging mass and wing length; Table 2.1).

2.3.2. Effects of manipulation on current reproductive investment

Abandonment following treatment was frequent, especially in the clipRT treatment group. Overall, 7 ctrl females (9.4%, n = 74), 8 ctrlRT females (11.9%, n = 67), and 24 clipRT females (49.0%, n =49) abandoned following capture during incubation ($\chi^2_{[3]} = 103.2$, $P < 0.001$). In 2013, 2 ctrl females (n = 27) abandoned, while 5 ctrlRT females (n = 14) abandoned ($\chi^2_{[2]} = 3.09$, $P = 0.08$). In 2014, 9 clipRT (n = 16) birds abandoned following the clipping treatment, whereas 1 ctrlRT (n = 16) females abandoned, and 4 ctrl (n = 15) females abandoned ($\chi^2_{[3]} = 9.67$, $P < 0.01$). Likewise, in 2015, 8 clipRT (n = 14) birds abandoned following the clipping treatment, whereas 1 ctrlRT (n = 15) females abandoned, and no ctrl (n = 16) females abandoned ($\chi^2_{[3]} = 17.74$, $P < 0.001$). Finally, in 2016, clipRT females abandoned (7 out of 19) at a much greater rate than both ctrl females (1 out of 16) and ctrlRT females (1 out of 22) ($\chi^2_{[3]} = 9.52$, $P < 0.01$).

Comparing ctrl females and ctrlRT females, mass loss between mid-incubation and mid-chick-rearing varied by year (model 1; treatment*year; $F_{2,75} = 5.15$, $P < 0.01$): mass loss was greater in ctrlRT females in 2014 ($t_{23} = 4.32$, $P < 0.001$) but not in 2013 or 2016 ($P > 0.05$ in both cases; Figure 2.1). Similarly for model 2, mass loss significantly varied amongst treatment groups within years (model 2; treatment*year; $F_{2,57} = 13.48$, $P < 0.001$). In 2014 and 2016 clipRT females had higher mass loss than ctrl females ($t_{15} = -3.37$, $P = 0.01$; $t_{15} = -2.68$, $P < 0.01$).

Average provisioning rate over the course of four years pooling all treatments was 4.71 ± 2.73 nest visits/30 minutes. Ctrl and ctrlRT females provisioned their chicks at the same rate, and provisioning rate between treatment groups did not change in all four years (model 1; treatment effect; $F_{1,87} = 0.41$, $P = 0.53$; treatment*year effect; $F_{3,87} = 2.10$, $P = 0.61$). Moreover, provisioning rate did not vary amongst all three treatment groups in 2014, 2015, and 2016 (model 2; treatment effect; $F_{2,78} = 0.24$, $P = 0.79$; treatment*year effect; $F_{4,78} = 1.94$, $P = 0.17$).

2.3.3. Effects of manipulation on current reproductive productivity

There was a significant treatment*year interaction for the effect of radio transmitters on brood size at fledging (model 1; $F_{3,133} = 3.99$, $P = 0.02$; Figure 2.2). CtrlRT females had lower brood size at fledging in 2016 ($t_{57} = 3.67$, $P < 0.01$) but not in 2013, 2014, or 2015 ($P > 0.05$ in all cases). Similarly, there was a treatment*year interaction for model 2 ($F_{4,119} = 4.20$, $P = 0.01$) for brood size at fledge, but also evidence for an additive effect of clipping on brood size at fledge. ClipRT females had a lower brood size at fledge than ctrlRT in 2014 ($t_{21} = -3.68$, $P = 0.01$), and lower brood size at fledge than ctrl females in 2016 ($t_{27} = -3.25$, $P = 0.04$) but there were no other significant pair-wise contrasts ($P > 0.05$).

There was a significant treatment*year interaction for the effect of radio transmitters on days 17 fledgling mass, tarsus length, and wing chord length compared to ctrl females in model 1 (mass, $F_{3,133} = 8.68$, $P < 0.01$; tarsus, $F_{3,133} = 14.48$, $P < 0.001$; wing chord length, $F_{3,133} = 3.46$, $P = 0.04$; Table 2.2). Fledgling mass for ctrlRT females, in 2016, was significantly lower than ctrl female fledgling mass ($t_{36} = 5.01$, $P < 0.001$). Whereas, fledgling mass did not differ between ctrl females and ctrlRT females in all other years ($P > 0.05$ in all cases). There was no effect of radio transmitter on tarsus length between ctrl and ctrlRT females in 2013 and 2014 ($P > 0.05$ in all cases). However, in 2015 and 2016 there was a significant radio transmitter effect on fledgling tarsus length ($t_{27} = 3.79$, $P < 0.01$; $t_{36} = 6.46$, $P < 0.0001$; respectively). While there was no radio transmitter effect on wing chord length in 2013, 2014, and 2015, ctrlRT females fledged chicks with smaller wing chord lengths in 2016 than ctrl females ($t_{36} = 3.64$, $P = 0.01$). Similarly in model 2, there was a treatment*year interaction on fledgling mass, tarsus length, and wing chord length including the additive effect of wing-clipping (mass, $F_{4,119} = 6.66$, $P < 0.01$; tarsus, $F_{4,119} = 8.42$, $P < 0.01$; wing chord, $F_{4,119} = 5.46$, $P = 0.01$). Fledgling mass, tarsus length, and wing chord length at day 17 was only significantly lower for clipRT females compared to ctrl females in 2016 (mass, $t_{27} = -4.01$, $P < 0.01$; tarsus, $t_{27} = -5.03$, $P < 0.001$; wing chord, $t_{27} = 4.37$, $P < 0.01$; $P > 0.05$ for all other pairwise contrasts).

2.3.4. Effects of manipulation on future fecundity and local return rate

In total, 57% of ctrl females, 56% of ctrlRT females, and 37% of clipRT females initiated a second brood ($\chi^{2}_{[2]} = 19.57$, df = 2, $P < 0.0001$). However, there was no significant differences for brood size initiation among treatments within years ($P > 0.05$ in all cases). Brood size at fledge for second broods did not differ between ctrl females and ctlrRT females (model 1; treatment; $F_{1,90} = 0.04$, $P = 0.84$; treatment*year; $F_{3,90} = 2.24$, $P = 0.12$) or when we compared among all three treatment groups in 2014, 2015, and 2016 (model 2; treatment; $F_{2,82} = 0.63$, $P = 0.55$; treatment*year; $F_{4,82} = 1.81$, $P = 0.19$).

There was a significant treatment*year interaction for the effect of a radio transmitters on cumulative brood size at fledge, or total chicks fledged year 1 + total chicks fledged the subsequent year (model 1; $F_{2,106} = 5.78$, $P < 0.01$; Figure 2.3). However, pairwise comparisons revealed no significant differences within a single year between ctrl females and ctrlRT females ($P > 0.05$ in all cases). Moreover, there was a significant treatment*year interaction on cumulative brood size at fledge when we analyzed years with ctrl, ctrlRT, and clipRT females (model 2; $F_{2,90} = 6.05$, $P = 0.03$;). In females treated in 2014 (an “intermediate” year), cumulative brood size at fledge was higher in ctrlRT females (7.18 ± 3.98 chicks) compared with clipRT females (3.25 ± 4.17 chicks; $t_{35} = -2.92$, $P = 0.04$), and ctrl females raised 4.46 ± 3.92 chicks (not significantly different from either other treatment, $P > 0.05$ in both cases). In females treated in 2015 (a “good” year), cumulative brood size at fledge was highest for ctrl females (8.38 ± 4.34 chicks), lowest for clipRT females (2.21 ± 2.61 chicks; $t_{29} = -4.42$, $P < 0.001$), and intermediate in ctrlRT females (4.54 ± 3.33 chicks; not different from either other treatment, $P > 0.08$ in both cases). Local return rate between successive years for all females was equal for both ctrl females (37%) and ctrlRT females (41%), but significantly less in clipRT females (30%) ($\chi^{2}_{[2]} = 17.79$, $P < 0.01$). However, there was no treatment effect within years ($P > 0.05$ in all cases).

2.4. Discussion

We analyzed the effects of handicapping on current reproductive investment (abandonment, mass change, provisioning rate), current productivity (brood size at fledge and chick quality), and future fecundity/survival (second brood size at fledge, cumulative brood size at fledge, and local return rate) over a four-year period to test the hypothesis that variation in response to manipulation can be explained by ecological context. We predicted that with an increased workload, i.e. an effect of radio-transmitter attachment and an additive effect of the wing-clipping, individuals would maintain their current reproductive investment and current reproductive productivity at a cost to future survival and fecundity. However, we also predicted that this 'decision' would vary depending on the quality ("good" vs. "bad") of the year. Across all years, in response to an increase in workload, clipRT individuals reduced current reproductive investment (mass loss), current productivity, and future survival/fecundity (Table 2.3). Within years, the response to treatment was varied but did not align clearly with our assessment of "good" to "bad" year. Although in 2013, (a "bad" year) there was no clipRT treatment, there was no difference in current reproductive investment, current productivity, or future fecundity/survival among control and radio-transmitter females. In 2014 (an intermediate year), clipRT females reduced current reproductive investment, current productivity, and future fecundity compared to ctrl females, and while ctrlRT females reduced current reproductive investment (increased mass loss) they had higher current and future productivity. In both 2015 and 2016 ("good" years), clipRT females reduced current reproductive investment compared to ctrl females. However, while there was no difference in current reproductive productivity amongst treatments in 2015 (although clipRT females had a lower cumulative brood size at fledge), both clipRT and ctrlRT females fledged fewer and lesser quality chicks than ctrl females in 2016.

Overall, current reproductive investment decreased with an increase in workload. ClipRT females consistently abandoned at a greater rate than ctrl and ctrlRT females. Other wing-clipping studies have also reported abandonment in clipped treatment groups (Harding et al., 2009; Rivers et al., 2017; Tieleman et al., 2008; Weimerskirch et al., 1999). In a study by Ouyang et al. (2012), great tits, *Parus major*, with higher corticosterone were more likely to abandon their breeding attempt. Therefore, an individual’s reproductive decision on whether to abandon the nest may be part of a stress response. In our study, since some individuals who immediately abandoned their clutch returned the following year (n = 6, or 15% of all abandonment), we know that this may represent an “adaptive” reproductive decision as opposed to simply death from the treatment.

For both clipRT and ctrlRT individuals that continued with parental care, in some years, mass loss greatly increased from capture during incubation to the middle of chick-rearing (day 10). Mass loss is a consistent response seen following wing-clipping treatment (Bijleveld and Mullers, 2009; Velando, 2002; Winkler and Allen, 1995), although other studies have reported no change in mass (Navarro and González-Solís, 2007; Tieleman et al., 2008). Mass change while chick-rearing is also variable in studies using an addition of a weight (cf. clipping); some studies report increased mass loss (Paredes et al., 2005; Weimerskirch et al., 2000), while other studies report no change in mass (Hegemann et al., 2013; Sæther et al., 1993). However, in our study, mass loss varied among treatment groups within years, but not in a way consistent with our assessment of year quality. In 2013 (a “bad” year) and 2016 (a “good” year), mass loss did not vary between ctrl females and ctrlRT females, whereas in 2014 (an “intermediate” year) mass loss increased for both ctrlRT females compared with ctrl females. Mass loss in females following the clipping treatment always increased.

In contrast to abandonment and mass change, a third measure of current investment, provisioning rate, was unaffected by the addition of a radio transmitter and the additive effect of wing-clipping both overall and within years. Change in chick feeding frequencies in response to clipping is widely varied in the literature. Similar to our study, many studies have found provisioning rate to not vary between clipped and control groups (Leclaire et al., 2011; Tieleman et al., 2008), while other studies reported a decrease in provisioning rate in clipped treatment groups (Sanz et al., 2000; Winkler and Allen, 1995). That said, provisioning rate fails to capture the intricacies of how individuals can alter their foraging behaviour (e.g. load size, prey type; (e.g. Wright et al., 1998); see Chapter 3).

Like current reproductive investment, current reproductive productivity generally decreased with an increased workload. Within years, productivity among treatment groups greatly varied, but again, in a way inconsistent with our assessment of year quality. In 2013 (a “bad” year), 2014 (an “intermediate” year), and 2015 (a “good” year), ctrl females and ctrlRT females fledged the same number of chicks, while ctrlRT females fledged significantly fewer chicks in 2016 (a “good” year). While clipRT females fledged significantly fewer chicks in 2014 (an “intermediate” year) and 2016 (a “good” year), there was no difference amongst all treatment groups in 2015. Interestingly, in 2014 (an “intermediate” year), ctrlRT females fledged more chicks than clipRT females, but otherwise there were no differences in the number of chicks fledged between ctrlRT and clipRT females. In addition to the number of chicks reared, there were inconsistent patterns of variation in quality of chicks at fledging. In 2013 (a “bad” year) and 2014 (an “intermediate” year), fledging mass and structural growth did not differ among treatment groups, whereas in 2016 (a “good” year), clipRT females and ctrlRT females fledged chicks with decreased mass, tarsus length, and wing chord length, and in 2015 (a “good” year) ctrlRT females fledged chicks with decreased structural growth (tarsus length). Again, the literature on the response to current productivity and chick condition following a clipping treatment is varied. Some studies have found that parents can maintain their nestling’s body mass and structural growth following a clipping treatment (Sanz et al., 2000; Winkler and Allen, 1995), while other studies found that chicks suffer the consequence of a clipping treatment (Bijleveld and Mullers, 2009; Leclaire et al., 2011; Tieleman et al., 2008). Likewise, studies that add a weight during chick-rearing report varied results. Sæther (1993) reported increased chick mortality following the addition of a weight while other studies report no change in chick condition (Hegemann et al., 2013; Weimerskirch et al., 2000).

While both current reproductive investment and current breeding productivity decreased with an increased workload, only clipRT females had decreased future breeding productivity and local return rate (caveat: return rate and subsequent breeding productivity for individuals in 2016 is not yet available and will be added to this analysis). Overall, clipRT females had a lower local return rate and lower cumulative brood size at fledge. We found, however, no differences among treatment groups in second brood size at fledge during the year of the treatment. As mentioned above, most wing-clipping studies only analyze data from a single breeding attempt. However, Winkler and Allen (1995) reported lower return rates for clipped individuals the following year, whereas Navarro and González-Solís (2007) found no difference in return rate. Other studies that added weights to chick-rearing adults found both lower resighting rates in clipped individuals (Paredes et al., 2005) and no change in resighting between treatment groups (Weimerskirch et al., 2000).

In summary, we found that with an increased workload associated with either a radio transmitter or clipping, individuals reduced current reproductive investment, current productivity, and future productivity/survival. However, reproductive decisions varied greatly among years and were sometimes counterintuitive (e.g. more negative effects on chick quality in a putative “good” year, 2016). This result is particularly important, since only a few wing-clipping studies include data from more than a single breeding season and typically assess effects of treatment based only on a single, current breeding attempt. Contrary to our prediction, individual’s decision did not align with our definition of “good” and “bad” years. Still, environmental conditions are known to alter reproductive decisions between years (Erikstad et al., 1998, 2009) and within years (Schifferli et al., 2014). Our study was carried out in years with highly variable productivity with variable response from individuals. Our results find a cost a reproduction, especially for clipped individuals, following an increased workload. Clipped individuals that continue to rear chicks following the manipulation were less likely to initiate a second brood, return the following year, and had lower future productivity. This study is one of a few that find a cost of reproduction to females in birds. Moreover, these results highlight the need to conduct workload manipulations over multiple years (since the response varied within years) to better understand when individuals make specific reproductive decisions.

2.5. References

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2.6. Tables

Table 2-1. Current reproductive productivity (number and size of offspring) for ctrl birds across all years (2013, 2014, 2015, and 2016).

	2013 ”bad year”	2014 “intermediate”	2015 “good year”	2016 “good year”	All Years
n females	25	14	16	16	71
Mean ± SD Julian date of 1st egg	96 ± 1.99	96 ± 1.99	89 ± 2.59	95 ± 2.20	95 ± 5.11
Mean ± SD brood sizes at fledging	2.70 ± 2.10	3.06 ± 1.91	4.58 ± 1.21	3.76 ± 1.98	3.46 ± 1.97
Mean ± SD fledgling mass (g)	73.73 ± 5.77	74.63 ± 3.76	73.80± 4.43	80.20 ± 2.58	75.39 ± 5.09
Mean ± SD fledgling tarsus length (mm)	33.72 ± 1.15	31.45 ± 2.70	33.52 ± 1.38	33.87 ± 0.61	33.32 ± 1.68
Mean ± SD fledgling wing chord (mm)	87.36 ± 5.49	88.72 ± 4.22	88.24 ± 1.91	94.78 ± 1.57	89.56 ± 4.62

Table 2-2. Current productivity (number and size of offspring) across treatments and years

	Mean ± SD brood sizes at fledging	Mean ± SD fledgling mass (g)	Mean ± SD fledgling tarsus length (mm)	Mean ± SD fledgling wing chord (mm)
2013:				
ctrl (n=25)	2.70 ± 2.10	73.73 ± 5.77	33.72 ± 1.15	87.36 ± 5.49
ctrlRT(n=14)	2.36 ± 1.39	74.79 ± 4.57	33.61 ± 1.47	87.89 ± 8.31
2014:				
ctrl (n=14)	3.06 ± 1.91	74.63 ± 3.76	31.45 ± 2.70	88.72 ± 4.22
ctrlRT(n=15)	4.60 ± 0.63	74.20 ± 3.65	32.99 ± 1.52	89.75 ± 3.48
clipRT (n=7)	2.22 ± 1.85	76.72 ± 3.27	33.29 ± 1.86	89.97 ± 3.51
2015:				
ctrl (n=16)	4.58 ± 1.21	73.80± 4.43	33.52 ± 1.38	88.24 ± 1.91
ctrlRT(n=12)	3.17 ± 1.40	76.69 ± 3.75	30.74 ± 1.27	87.82 ± 5.48
clipRT (n=6)	3.50 ± 1.87	74.43 ± 7.78	31.60 ± 2.67	90.04 ± 4.92
2016:				
ctrl (n=16)	3.76 ± 1.98	80.19 ± 2.58	33.87 ± 0.61	94.78 ± 1.57
ctrlRT(n=21)	2.38 ± 1.98	71.08 ± 6.54	29.65 ± 2.76	87.81 ± 5.12
clipRT(n=12)	2.42 ± 1.83	72.09 ± 6.26	29.71 ± 2.02	86.98 ± 6.01
Total:				
ctrl (n=71)	3.61 ± 1.79	75.39 ± 5.09	33.32 ± 1.68	89.56 ± 4.62
ctrlRT n=62)	3.06 ± 1.73	74.01 ± 5.05	31.73 ± 2.47	88.46 ± 5.40
clipRT(n=25)	2.59 ± 1.84	73.99 ± 6.14	31.07 ± 2.55	88.49 ± 5.21

Table 2-3. Overview of all traits measured for all treatments along a workload gradient overall and per year

	Trait	ctrl	ctrlRT	clipRT
			Increasing workload	
Current Investment	Abandonment		+All Years, +2014, +2015, +2016	
	Change in mass (g) mid-chick-rearing		[2014], +2016, omit 2015	
	Provisioning rate		None	
Current Productivity	Brood size at fledge		-2014, [2016]	
	Fledgling mass (g)		[2016]	
	Fledgling tarsus length (mm)		(2015), [2016]	
	Fledgling wing chord length (mm)		[2016]	
Future Productivity	2nd brood size at fledge		None	
	Cumulative brood size at fledge		+2014, +2015	
	Return Rate		+All Years	

+ denotes significant change with the predicted increase in workload with clipRT individuals only

- denotes significant change but opposite to the predicted increase in workload

[] denotes partial significant change with the predicted increase in workload; however, no additive effect

() denotes significant change with the predicted increase in workload but only for ctrlRT individuals

2.7. Figures

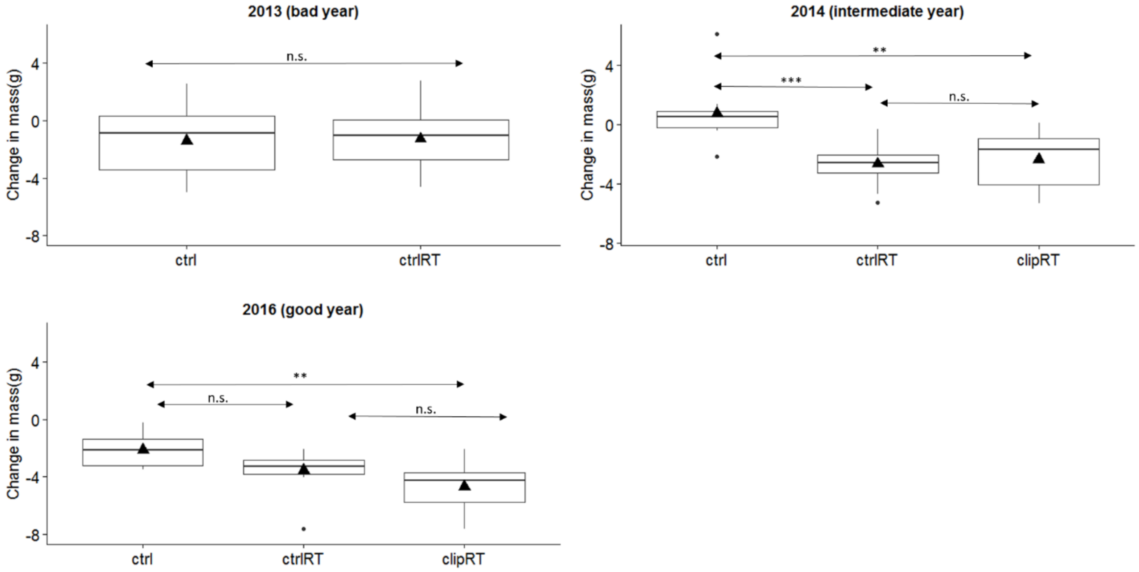

Figure 2-1. **Change in mass from mid-incubation to the middle of chick-rearing (day 10) in all treatment groups in years 2013, 2014, and 2016. We did not recapture females during chick-rearing in 2015. The * represent statistical significance. The triangle indicates the mean.**

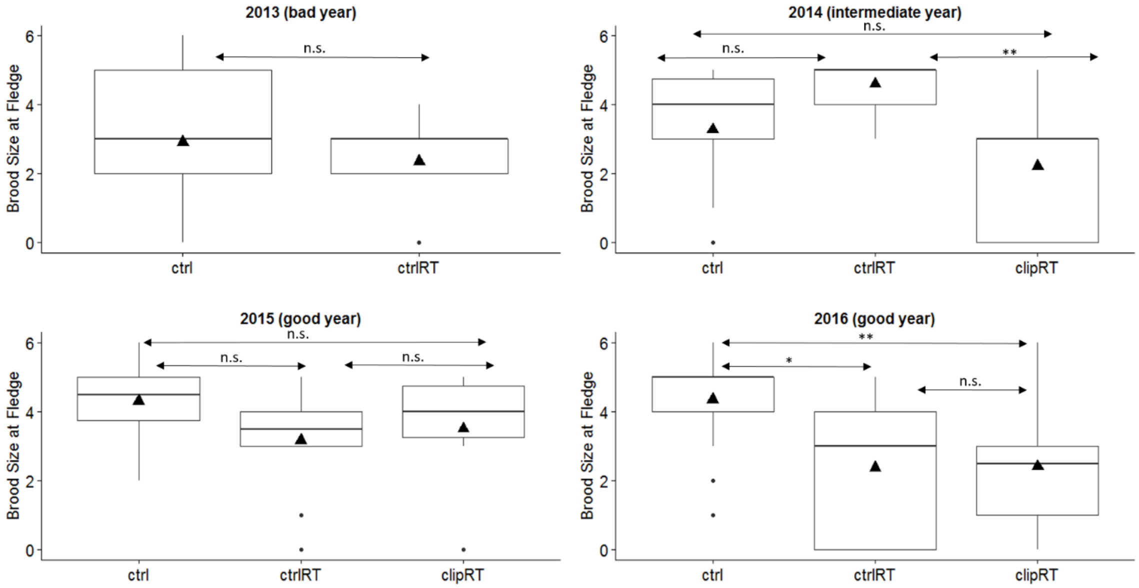

Figure 2-2. **Brood size at fledge (first brood) for all treatment groups by year. The * represents statistical significance. The triangle indicates the mean.**

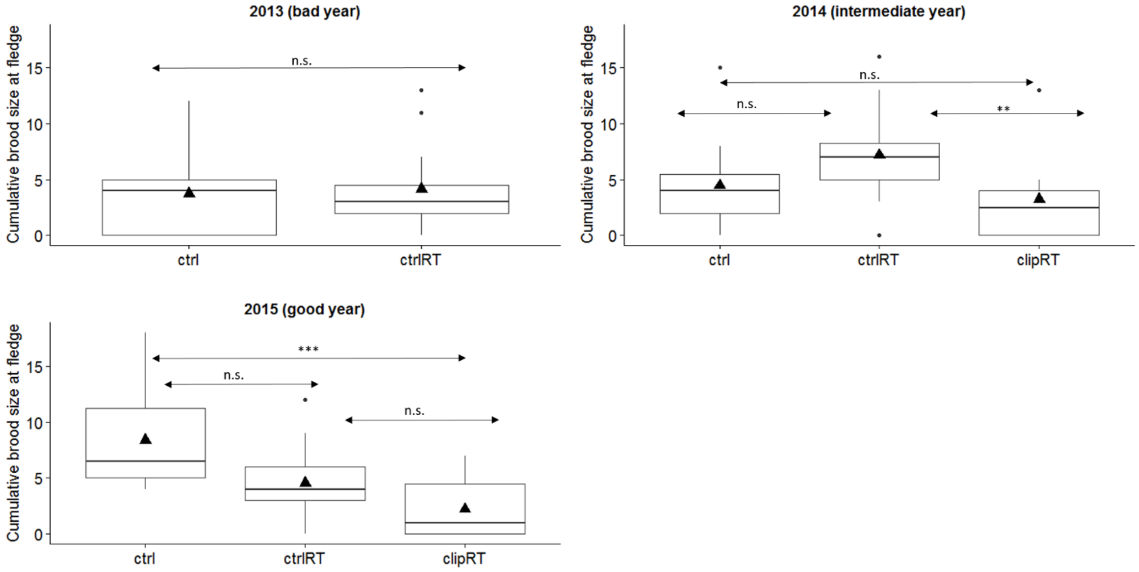

Figure 2-3. **Cumulative brood size at fledge (total chicks fledged year 1 + total chicks fledged the subsequent year) for individuals first captured in 2013, 2014, and 2015. The * represents statistical significance. The triangle indicates the mean.**

Chapter 3.

Individual variation in activity of chick-rearing birds using an automated radio telemetry system

3.1. Introduction

The trade-off between survival and reproduction is central to life-history theory: individuals must balance resource allocation towards current reproductive effort, future reproduction, and survival (Stearns 1989). Individuals that invest more resources into current reproduction should benefit by raising more and better quality offspring, however those same individuals might pay a cost of increased parental effort in terms of reduced future fecundity and/or survival (Clutton-Brock et al. 1983). Rather surprisingly, there is little evidence to support this trade-off, particularly in females (reviewed in Santos and Nakagawa 2012). One reason for this might be that, historically, provisioning rate has been used to measure parental effort, mainly in birds (e.g. Bryant 1988; Mariette et al. 2011; Nur 1984). Using this metric, evidence that increased provisioning rate leads to fitter chicks is equivocal (Moreno et al. 1995; Nur 1984; Schwagmeyer and Mock 2008; Williams, 2012, but see Mackas et al. 2010), despite the fact that there is marked (5-10-fold) individual variation in provisioning rate in chick-rearing birds. For example, blue tits *Cyanistes caeruleus* visit their nests between 300 and 1,500 times per day (Nur, 1984), individual house sparrows *Passer domesticus* make 5-45 food deliveries per hour to their chicks (Schwagmeyer and Mock, 2008), and the provisioning rate of female European starlings feeding 6-8-day old nestlings varies almost 10-fold, from 1.0 to 9.33 visits every 30 minutes (Williams, 2012).

Although provisioning rate is the most commonly used metric to measure parental workload in birds, it might fail to capture the many ways in which individual birds can alter their foraging behaviour (Stephens et al. 2007; Wright et al. 1998) such that the overall energetic or physiological cost of foraging may differ for two individuals delivering the same amount of food to their chicks (Collins et al. 2016). During chick-rearing, provisioning birds can adjust their foraging behaviour in many other ways, e.g. varying load size, prey type, foraging distance, and activity (Krebs, 1999; Mariette et al. 2011; Schwagmeyer and Mock 2008; Stauss et al. 2005; Wright et al. 1998; Weimerskirch et al. 1995). As examples, thin-billed prions, *Pachyptila belcheri*, adjust load sizes relative to the length of their foraging trips at sea (Weimerskirch et al. 1995), and European starlings change their prey selection and load size depending on the brood size (Wright et al. 1998). Without fully understanding these potential adjustments in foraging behaviour in relation to increased parental effort, it might be difficult to correctly interpret physiological and fitness costs of increased workload (Bryant 1988; Harding et al. 2009; Mariette et al. 2011; Stephens et al. 2007). Very few studies have obtained data on a combination of measures of foraging in chick-rearing birds (but see García-Navas and Sanz 2011; Mariette et al. 2011; Schwagmeyer and Mock 2008), especially for large numbers of individuals that would allow robust assessment of individual variation in how birds deal with workload during parental care.

As described above, mainly due to logistical issues, most studies of parental workload have focused on activities at the nest (i.e. nest visit rate provisioning behavior) (but see Mariette et al. 2011; Stauss et al. 2005). However, recent technological developments now allow researchers to monitor individual free-living animals 24/7 (Wilmers et al. 2015). Automated radio telemetry allows for the collection of daily activity data of individuals over an extended period of time and has been used to quantify nocturnal extraterritorial forays (Ward et al. 2014); fever and sickness behaviour in sparrows (Adelman et al. 2010); and activity rhythms under constant daylight in the arctic (Steiger et al. 2013). However, this technology has yet to be used to quantify parental activity, or workload, in chick-rearing birds in relation to breeding productivity. Also, most studies quantifying parental activity, or workload, restrict their analysis to a short window, typically 30-minute observations over the course of a couple of days during the chick-rearing period (García-Navas and Sanz 2011; Mariette et al. 2011; Schwagmeyer and Mock 2008; Stauss et al. 2005). Automated radio telemetry can monitor individual activity during parental care remotely throughout the entire breeding period.

Here, we used an automated radio telemetry system to determine the activity of individual female European starlings from late incubation through the entire chick-rearing period. We combined radio tracking with a) video analysis of prey brought back to the nest, and b) a handicapping experiment (wing-clipping) to investigate changes in foraging behaviour in response to experimentally-increased workload. Specifically, we first address whether handicapped individuals decrease their investment in their current reproduction bout in terms of number and size of offspring. We then tested whether the clipped individuals mediate the effect of their handicap by looking at a variety of foraging behaviour metrics (i.e. provisioning rate, prey type, load size, and activity). Finally, we tested whether handicapped females paid a physiological cost (measured in body condition) leading to a reduction in future reproductive investment (i.e. double brooding and productivity the following year). We predicted that individual females subject to wing-clipping would maintain their current breeding productivity by altering their foraging behaviour. This could be facilitated in a myriad of ways. For example, clipped females may decrease their provisioning rate while increasing the number of prey delivered. We also predicted that this change in behaviour would come at a cost. Clipped individuals who maintain breeding productivity by changing their foraging behaviour will suffer in terms of their physiological condition and reduced future productivity.

3.2. Methods

3.2.1. Breeding data

We collected breeding data on European starlings from March through June in 2015 and 2016 from our long-term study population at Davidstead Farm, Langley, British Columbia, Canada (49°10’N, 122°50’W). The field site contains about 150 nest boxes mounted on posts around pastures and on farm buildings. Each year, we followed the same basic field protocol: nest boxes were checked daily from late March to determine laying date and clutch size. Hereafter, clutch size denotes the number of eggs laid, whereas brood size refers to the number of chicks alive in the nest. Nests were monitored until either failure or fledging to quantify productivity. Each nest was checked on day 17 (shortly prior to fledging) to obtain brood size at fledging. Fledgling mass, tarsus, and wing chord were all measured on day 17. Individual breeding females were captured during mid-incubation, measured (mass, tarsus, wing chord), and fitted with color bands and individually numbered metal bands (Environment Canada # 10646). Some females (2015: n = 30; 2016: n = 42) were fitted with a digitally-coded radio transmitter (Lotek Wireless Inc.) by means of a leg loop harness (Rappole and Tipton 1991). The weight of the transmitters (≤ 2.1g) is less than the suggested 5% of the body weight threshold given the average mass of female European starlings during these years was 82.9 g (Naef-Daenzer 1993). Transmitters had a battery life of at least 90 days. Males were not captured or banded, therefore their identity is unknown, but we obtained diet and provisioning data for focal males visiting specific nest boxes. We repeated this process during the second brood window, beginning ~31 days (10 days of incubation, 21 days to fledging) after clutch completion of the earliest first clutch. Individuals captured the following year were monitored for future productivity analyses using the same procedure. We assigned individuals to three treatment groups, non-manipulated control females (ctrl), control females with radio transmitters (ctrlRT), and clipped females with radio transmitters (clipRT).

3.2.2. Provisioning data

Parental provisioning were determined via observations conducted from 09:00 to 14:00 on days 6, 7, 8, and 12, 13, 14 post-hatching for 30 minutes (day 0 was defined as the day the majority of chicks in the nest hatched). The timing of observations was standardized (see Fowler & Williams 2015 for more details).

In addition, for all nests of radio-transmitter birds, we deployed video cameras (Canon VIXIA HF R52) which were placed approximately 5 meters from each nest box on days 6-8 and 12-14 post-hatching for a duration of at least 35 minutes. Videos were analyzed using VLC Media Player, which allows for pausing or slowing down video playback. Only 30 minutes of the video were analyzed and the first 5 minutes were used as a buffer between disturbances at the nest. For each nest visit by parent birds, we recorded the number and type of prey.

3.2.3. Wing clipping

Adult females were caught during mid-incubation and alternately assigned to either a clipRT treatment or a ctrlRT treatment with the exception that clipRT females from 2015 who returned in 2016 were automatically assigned as controls in 2016 (n =4). There was no difference in laying date ($p = 0.39$, $t = 0.87$, df = 71), clutch size ($p = 0.18$, $t = -1.36$, df = 71) or body mass at incubation ($p = 0.81$, $t= 0.23$, df = 71) for females subsequently assigned to each treatment. Birds assigned to the clipRT treatment had every third primary feather (i.e. primaries 3, 6, and 9) from each wing removed near its base with scissors. We estimated average wing surface area from wing photos for both wings = 142 cm^2 and mean body mass = 82.9 g, so wing loading in non-manipulated adults = 82.9 g/142 cm^2 = 0.583 g/cm^2. Adding a 2 g radio transmitter with no change in body mass increases estimated wing loading to 0.597 g/cm^2 (+ 1.2%). However, birds lost 3.3 g on average by the chick-rearing stage, so wing loading would actually be lower (-0.5%). Calculating the effect of wing-clipping is more complicated: when wings were held in a natural, relaxed position, gaps between feathers due to removal of primaries 3, 6, and 9 were not evident because adjacent feathers overlapped; estimated surface area for outlined wings was only -0.8% lower in clipped birds ($P > 0.05$). When we stretched wings out so that gaps were accentuated and drew an outline around the gaps, wing area was, on average, 17.7% lower after clipping. This resulted in estimated wing-loading = 0.696 before mass loss (+21%), and 0.675 after mass loss (+ 17%). This estimation therefore represents a maximum magnitude of effect, but likely one that is biologically unrealistic since it ignores any behavioural adjustments birds can make (changes to wing angle, feather orientation) which would affect the aerodynamic properties during actual flight to compensate for lost feathers. Nevertheless, with increased wing-loading, clipped birds would clearly be more aerodynamically challenged than non-clipped birds, increasing costs of foraging flights. The effect of this treatment is temporary, as individuals replace these feathers during the post-breeding moult (August-October). On day 10 post-hatching, females were re-captured and weighed again.

3.2.4. Automated radio telemetry

For the duration of the breeding season, five (2015) or four (2016) Automated Receiving Units (ARUs; Lotek Wireless Inc., Newmarket, Ontario, Canada) with two to four 5-element Yagi antennas were stationed around the field site to allow for continuous reception of radio signals from tagged individuals. The receivers were placed strategically throughout the study site as to capture all of the nest boxes and potential foraging areas (based on preliminary hand-held tracking in 2013-14, M. Fowler unpub. data; Figure 3.1). Every 8 seconds, each antenna at each tower alternately scanned for each deployed radio transmitters, which allowed for the activity of the tagged females to be monitored on a continuous basis. Estimated from human validation, radio signals were detected up to distances of approximately 1 km, greater than the distance from one end of the field site to the other (~800m).

We calculated "activity" of females during foraging and provisioning of chicks following methods described in Steiger et al. (2013), Ward et al. (2014), and Zúñiga et al. (2016). We used the ARU and antenna closest to the focal nest box, i.e. with the strongest average signal of a given individual for all activity analyses of that subsequent individual (preliminary analysis showed that using any other antenna gave quantitatively similar results for activity estimates; Figure A1). Lotek receivers use Power as a received signal strength indicator (RSSI) (1 RSSI value, or Power, is approximately 2.2 dBm; Lotek Wireless Inc. pers. comm.). We applied a minimum threshold of a Power of 50 to control for background noise, which when converted to signal strength is consistent with previous studies that calculate activity (Steiger et al. 2013; Ward et al. 2014; Zúñiga et al. 2016). We tested whether estimated activity was dependent on choice of specific threshold values, but activity using Power thresholds of 30 and 10 were highly correlated with using a threshold Power of 50 (see appendix Figure A2 and Figure A3).

The Power of an inactive bird is relatively constant from one detection to the next, resulting in a relatively low variance in Power, whereas Power varies greatly from one detection to the next when an active bird moves relative to a stationary antenna (Greives et al. 2015; Ward et al. 2014). We used the change (Δ) in Power from one detection to the next to determine if a bird was active or inactive. We determined threshold values for Δ Power by observing the Δ Power of incubating, or inactive, females. A Δ Power ≤ 10

indicates an inactive bird. This value is equal to the upper end of the 99% confidence interval of the mean for observed incubating birds. Note that using a threshold of ∆ Power 10 and ∆ Power 5 gave quantitatively similar results (see appendix Figure A4). Moreover, ∆ Power 10 threshold when converted to signal strength (4.5 dBm) is similar to values used in previous studies as thresholds for “activity” (Adelman et al. 2010; Steiger et al. 2013; Ward et al. 2014). An individual’s activity over a day was calculated by dividing the number of “active” readings over all detections throughout the day. Time intervals were split between hours of daytime and nighttime using civil twilight data (The National Research Council Canada, http://www.nrc-cnrc.gc.ca/eng/services/sunrise/). In addition, many individuals bit off their radio antenna. Birds with fewer than 8 days of activity data, due to tag failure, were excluded from the activity analyses. Any individual that was not detected for the entirety of the chick-rearing period was removed from the analyses on the effects of the number of prey and prey type on activity.

3.2.5. Statistical analysis

All analyses were completed in R STUDIO version 0.98.1028 (R Studio Team 2015) using lsmeans (Lenth 2016), lme4 (Bates et al. 2014), lmtest (Zeileis and Hothorn 2002), nlme (Pinheiro et al. 2013), stats (R Studio Team 2015), and multcomp (Hothorn et al. 2008). In general we used linear mixed-effects models to compare variation in activity, breeding productivity, and foraging metrics while controlling for year as a covariate. We used individual (band number) as a random factor. Individuals who abandoned immediately following the treatment were excluded from current investment and productivity analyses. However, since some individuals returned the following year after abandoning, they were included in future productivity analyses. Analysis of mass loss was done using general linear models. Analyses for mass loss was restricted to the number of individuals that we could recapture (n = 29). For the partial brood loss analysis, individuals were categorized into females with partial brood loss and females without partial brood loss.

3.3. Results

3.3.1. Effects of manipulation on current reproduction

In 2015, of the 30 radio tagged females, 11 deserted immediately after tagging (10 of which were clipRT) but 2 of these individuals eventually relayed. In 2016, of the 42 radio tagged females, 8 deserted immediately (7 of which were clipRT) and 4 of those individuals eventually relayed (Pooling both years; $\chi^2 = 14.28$, df = 1, $P < 0.001$). While there was a strong treatment effect, there was no year effect between treatment groups on abandonment ($P > 0.05$). There was no significant difference in mass ($t_{71} = 1.45$, $P = 0.15$), lay date ($t_{71} = 0.02$, $P = 0.98$), or clutch size ($t_{71} = 1.28$, $P = 0.21$) between individuals that deserted and individuals that continued parental care.

Mean brood size at fledging, including individuals that abandoned their nest following clipping, decreased significantly for females from ctrl, ctrlRT, to clipRT treatments ($F_{2,108} = 18.10$, $P < 0.0001$; Table 3.1). Brood size at fledging was significantly higher for ctrl vs. ctrlRT ($t = 3.46$, $P < 0.01$), ctrl vs. clipRT ($t = -5.98$, $P < 0.001$), and for ctrlRT vs. clipRT ($t = 2.58$, $P < 0.05$). When individuals who immediately abandoned their nest are removed from the analysis there is still an overall treatment effect on brood size at fledge ($F_{2,89} = 4.48$, $P = 0.04$). However, excluding individuals who immediately abandoned, there was no significant difference for brood size at fledging between ctrlRT and clipRT females, or between ctrl and ctrlRT females ($P > 0.15$ in both cases) but clipRT females fledged significantly fewer chicks than ctrl females ($t = -2.86$, $P = 0.01$).

There was an overall treatment effect on day 17 fledgling mass, tarsus length, and wing chord ($F_{2,275} = 4.7$, $P < 0.01$; $F_{2,275} = 68.29$, $P < 0.0001$; $F_{2,275} = 6.69$, $P < 0.01$; respectively). Fledging mass, tarsus length, and wing chord were all significantly greater in ctrl females compared with both ctrlRT and clipRT individuals ($P < 0.05$ in all cases). However, there was no significant difference in these same measurements comparing ctrlRT and clipRT individuals ($P > 0.05$ in all cases; Table 3.1).

Mass loss between mid-incubation and the middle of the chick-rearing period increased with the predicted experimental increase in workload ($F_{2,28} = 7.34$, $P < 0.01$). On average ctrl females lost 2.12 g ± 1.43 g (n = 12) whereas mass loss was significantly greater in clipRT females (4.73 g ± 1.73; n =8; z = 3.78, $P < 0.001$). CtrlRT females lost 3.54 g ± 1.51 g (n = 11) and mass loss was intermediate to, and not significantly different from, either ctrl females (z = 2.21, P = 0.07) and clipRT females (z = 1.73, P = 0.19).

3.3.2. Effects of manipulation on provisioning rate and diet

Female provisioning rate increased with chick age from days 6-8 (4.1 ± 2.7 nest visits/30 minutes) to days 12-14 (5.4 ± 3.5 nest visits/30 minutes; $F_{1,102} = 8.16$, $P < 0.01$). In contrast, male provisioning rates were much lower and did not change with chick age: days 6-8, 1.5 ± 2.1 nest visits/30 minutes; days 12-14, 1.6 ± 2.2 nest visits/30minutes ($F_{1,102} = 0.05$, P = 0.82). There was no overall treatment effect for female or male provisioning rate on days 6-8 ($F_{2,68} = 0.42$, P = 0.66; $F_{2,68} = 2.10$, P = 0.14) or on days 12-14 ($F_{1,34} = 0.83$, P = 0.36; $F_{1,34} = 0.08$, P = 0.78). Mean provisioning rate for both females and males however, significantly increased as brood size increased ($R^2 = 0.10$, t = 2.64, P = 0.01; $R^2 = 0.18$, t = 3.71, $P < 0.01$).

Overall we obtained data on 1,015 individual meals containing 1,927 prey items from 35 individual females (this information was only obtained for ctrlRT and clipRT females). Tipulid larvae (*Tipula paludosa*), black soldier flies (*Hermetia illucens*), and rat-tailed maggot larvae (*Eristalis tenax*) comprised approximately 98% of the chick's diet. Tipulid larvae was the most common meal (74% of all diet items), followed by black soldier flies (13%), and then rat-tailed maggot larvae (11%). However, there was no effect of wing-clipping treatment on the percentage of prey types brought back to the nest ($\chi^2_{[1]} = 3.01$, $P > 0.05$). There was also no effect of wing-clipping treatment on the number of prey brought back to the nest. On average ctrlRT females brought back 11.12 ± 4.41 prey items/30 minutes, whereas clipRT brought back 12.89 ± 6.20 prey items/30 minutes ($F_{1,34} = 0.99$, P = 0.32). Males contributed fewer total prey to chick feeding: males with a ctrlRT partner brought back 3.99 ± 5.06 prey items/30 minutes while males with a clipRT partner brought back 3.68 ± 3.83 prey items/30 minutes ($F_{1,34} = 0.04$, P = 0.85).

3.3.3. Effects of manipulation on activity measured with ARU detections

Overall activity, measured as % “active” detections, varied significantly with breeding stage and time of day (day/night): incubation/day-time, 12.0 ± 5.0% active detections, chick-rearing/day-time, 27.7 ± 10.3% active detections, incubation/night-time, 2.7 ± 4.1% active detections, and chick-rearing/night-time, 2.7 ± 4.1% active detections ($F_{3,772} = 5.2$, $P < 0.001$; Figure 3.2). Individual variation in activity during incubation was positively correlated with individual variation in activity during chick-rearing ($R^2 = 0.42$, $F_{1,21} = 15.44$, $P < 0.001$; Figure 3.3).

During late incubation (days 8-11), activity did not vary significantly by day ($F_{3,37} = 1.29$, $P = 0.29$) and there was no effect of wing-clipping treatment on activity: ctrlRT females, 12.3 ± 5.3% active detections versus clipRT females, 11.4 ± 4.7% active detections ($F_{1,20} = 0.73$, $P = 0.40$). We therefore averaged incubation activity per individual for subsequent analyses. Although there was considerable inter-individual variation in incubation activity, this variation neither explained the duration of incubation ($F_{1,20} = 0.13$, $R^2 = 0.01$, $P = 0.72$) nor partial brood loss (logistic regression; $z = -0.16$, $P = 0.87$).

We detected a low, but individually variable, level of activity at night and this was independent of breeding stage: 2.9 ± 2.0%, 3.5 ± 3.3, and 4.6 ± 5.5% active detections for incubation, chick-rearing, and post-fledging activity, respectively ($F_{2,372} = 1.28$, $P = 0.28$). Nighttime activity also did not differ between ctrlRT individuals (3.5 ± 3.9% active detections) and clipRT individuals (3.27 ± 2.4% active detections) during chick-rearing ($F_{1,22} = 0.02$, $P = 0.89$). An individual’s activity at night was not correlated with that same individual’s activity during the day ($R^2=0.01$, $F_{1,260} = 3.21$, $P = 0.07$).

There was a highly significant treatment*day interaction for diurnal activity during the chick-rearing period (days 0-21; $F_{21,361} = 2.22$, $P < 0.01$; Figure 3.4). Activity, for ctrlRT females increased from day 0 to 13, plateaued from day 13 to 16, and then slowly decreased until chicks fledged on day 21 (Figure 3.4). In comparison, activity for clipRT females hardly varied, and the treatment effect was greatest between days 6-20 post-hatching.

Although, on average, both female provisioning rate and activity increased from days 6-8 to days 12-14 (see above), there was no correlation between the provisioning rate on a given day and that same individual's activity that day ($R^2 = 0.02$, $F_{1,81} = 1.62$, $P = 0.21$; Figure 3.5). Furthermore, there was no correlation between activity level and either the average total number of prey items brought back to the nest per 30 minutes ($R^2 = 0.0002$, $F_{1,14} = 0.003$, $P = 0.95$; Figure 3.6c), or the average number of preferred prey items (tipulid larvae) brought back per 30 minutes ($R^2 = 0.0002$, $F_{1,14}=0.003$, $P = 0.95$; Figure 3.6a). However, activity was positively correlated with the average number of black solider flies brought back to the nest per 30 minutes ($R^2 = 0.51$, $F_{1,14} = 15.12$, $P < 0.01$; Figure 3.6b). In contrast to provisioning rate, total average activity did not increase as brood size increased ($R^2 = 0.03$, $F_{1,23} = 0.55$, $P = 0.47$). Finally, individual variation in activity did not predict either fledgling mass, tarsus length, or wing chord length ($P > 0.05$ in all cases; Figure 3.7).

3.3.4. Future costs to manipulated workload

Brood size at fledge for second broods, in the same year as the treatment, decreased with the predicted experimental increase in workload ($F_{2,38} = 11.68$, $P < 0.001$; Figure 3.8). On average ctrl females fledged 3.41 ± 1.37 (n=17) chicks from their second brood, whereas ctrlRT and clipRT females fledged significantly fewer chicks on average, 1.5 ± 1.78 (n=14) and 0.80 ± 1.14 (n=10) respectively ($t = 3.58$, $P < 0.01$; $t = -4.43$, $P < 0.0001$, respectively). There was no significant difference between the number of chicks fledged from the second brood between ctrlRT and clipRT females ($t = -1.14$, $P = 0.49$).

Total brood size at fledge for the following year decreased with the predicted increase in workload from the previous year, i.e. there was a long-term effect of wing-clipping treatment even in birds that survived to the following year (based on 1 year of data; $F_{2,71} = 3.01$, $P = 0.05$). Ctrl females fledged on average 8.5 ± 2.3 chicks the following year, while ctrlRT and clipRT females fledged significantly fewer chicks, 3.8 ± 1.3 and 1.7 ± 1.5, respectively ($t = 4.12$, $P < 0.001$; $t = -5.13$, $P < 0.0001$; Figure 3.8). Again, there was no significant difference in total brood size at fledge the following year between ctrlRT females and clipRT females ($P > 0.05$).

Considering the total number of chicks fledged during the year of the treatment and the following year, there was a decrease in the cumulative number of chicks fledged over 2 years with the predicted experimental increase in workload ($F_{2,71}$ = 14.21, $P < 0.01$). Ctrl females fledged on average 8.95 ± 4.34 chicks, ctrlRT females fledged 6.07 ± 3.27 chicks, and clipRT females fledged on average 3.88 ± 2.29 chicks. Cumulative productivity over the two years was significantly greater for ctrl females than clipRT females ($t = -3.27$, $P < 0.01$), but not for ctrlRT females ($t = 2.22$, $P = 0.07$; no difference for ctrlRT females and clipRT females $t = -1.25$, $P = 0.36$; Figure 3.8).

3.4. Discussion

In this study, we experimentally-increased workload of female European starlings during chick-rearing and analyzed their corresponding change in foraging behaviour using a novel automated radio-tracking system. We predicted a classic trade-off between reproduction and self-maintenance. More specifically, we predicted that wing-clipped females with an increased workload would alter their foraging behaviour in order to maintain their current reproductive bout, but that would come at a cost to future breeding productivity. Long-lived birds may decide to save their energy and reproduce the subsequent breeding season; however, starlings are relatively short-lived passerines (2-4 years at our field site), so they have a low probability of a subsequent breeding attempt. When including all individuals in the analysis, there was a decrease in current productivity with an increase in manipulated workload (ctrl to ctrlRT to clipRT). However, when individuals who abandoned the nest immediately after manipulation were removed from the analysis, only clipRT females had a lower productivity than ctrl females, and there was no difference in productivity between ctrlRT females and clipRT females. Consistent with previous studies and what we know about parental care, female starlings were most active while chick-rearing compared to late incubation and nighttime, suggesting we are obtaining biologically relevant behaviour (Bevan et al. 1995; Montevecchi et al. 1992). Given the difference in activity over the two breeding stages, we can conclude that we are obtaining accurate variation in individual behaviour. However, activity was not correlated with behaviour directly related to parental care (provisioning rate, number of prey, and prey type) or the outcome of behaviour directed towards parental care (brood size and fledgling size). Therefore, activity is also measuring non-parental care-related activities during chick-rearing, possibly elucidating rarely seen self-maintenance behaviour during chick-rearing. Finally, there was a decrease in future productivity (i.e. second brood productivity and productivity the following year) with the predicted increase in workload.

Here, automated radio tracking revealed interesting behaviour during parental care. There was marked inter-individual variation in incubation activity. Activity was highly repeatable from incubation to chick-rearing, suggesting that some individuals are simply more active than others throughout the entire breeding period, perhaps reflecting inherent phenotypic variation in individual quality. Various studies have reported repeatability in nest visit rate within years; however, female nest visit rate is often less repeatable or not repeatable at all (Cleasby et al. 2013; Nakagawa et al. 2007; Schwagmeyer and Mock 2003). In addition, there was also noticeable inter-individual variation in nighttime activity. While we don't have evidence to demonstrably show what individuals were doing at night, Ward et al. (2014) used an automated radio telemetry system to quantify extraterritorial forays at night in a diurnal yellow-breased chat, *Icterina virens*. For females, extraterritorial forays are most frequent when they are fertile (Chiver et al. 2008; Double and Cockburn 2000). If female European starlings were engaging in extraterritorial forays, then we would have expected nighttime activity to vary by breeding period and specifically be lower during times of high chick-rearing demand. Nighttime activity, nonetheless, did not vary by breeding stage. On the other hand, since our field site is on a dairy farm, it is illuminated at night with artificial light. Other studies have shown that artificial night light alters reproductive physiology, dawn song, lay date, and foraging in diurnal birds (Dominoni et al. 2013; Kempenaers et al. 2010; Santos et al. 2010). In contrast, individual variation in activity during the chick-rearing period was repeatable and predictably increased as chick sizes and demand increased (A. Cornell unpub. data). These results are consistent with other studies showing repeatability of nest visit rate during a breeding attempt and further suggests that activity data here is biologically meaningful (Dor and Lotem 2010; Gray et al. 2005).

Nest abandonment occurred at a much greater rate in clipRT females than both ctrlRT and ctrl females suggesting an additive effect from the clipping treatment. Likewise, nest abandonment has been shown to correlate with individual condition (Ouyang et al. 2012). Similar to other studies, ctrl females had a greater productivity and fledged better quality chicks than clipped females (in this study both ctrlRT and clipRT females), suggesting that both treatment groups passed on the cost of an increased workload to their chicks (Bijleveld and Mullers 2009; Navarro and González-Solís 2006; Tieleman et al. 2008; Wegmann et al. 2015). Despite the additive effect of clipping, there was no significant difference between the productivity and quality of the chicks between ctrlRT and clipRT females. In fact, several other studies found that individuals maintained their productivity following a clipping treatment (García-Navas and Sanz 2011; Ringsby et al. 2009; Rivers et al. 2017; Winkler and Allen 1995).

Due to the finding that there was no additive effect of clipping on productivity, our data suggests that by maintaining their reproductive output, individuals were bearing the brunt of the increased workload from the clipping, i.e. decreasing self-maintenance, as opposed to passing extra costs on to their offspring. We found that given an increased workload, female mass loss increased when measured during the middle of chick-rearing. Numerous studies have found a decrease in mass loss following a clipping treatment (Velando 2002; Winkler and Allen 1995; Weimerskirch et al. 1995), although other studies have reported no change in mass (Velando and Alonso-Alvarez 2003; Weimerskirch et al. 1999). A decline in body mass while chick-rearing could be a consequence to a reduced foraging ability due to wing-clipping, i.e. a cost. However, mass loss may also be interpreted as adaptive. Mass loss may be explained as an optimization of wing loading to maintain foraging efficiency (Lind and Jakobsson 2001; Norberg 1981). While it is difficult to determine the exact cause of the mass loss, the mass loss will negatively affect the clipped bird's ability to adjust to abrupt changes in food supply or inclement weather.

Despite the predicted increase in workload, there was no difference in the provisioning rate of females between treatments during days 6-8, and no difference in provisioning rate between ctrlRT and clipRT females during days 12-14 (we did not measure provisioning rate for ctrl females on days 12-14). The response to wing-clipping in terms of provisioning behaviour reported in the literature is highly variable. Leclaire et al. (2011) and Tielman et al. (2008) found that wing-clipped females fed their chicks at the same rate as control females, whereas Sanz el al. (2000) and Weimerskirch et al. (1994) found that clipped females significantly reduced their provisioning rate compared to controls. With that being said, provisioning rate appears to be unrelated to other measurements of parental effort (i.e. load size and prey type) (Sanz et al. 2000; Slagsvold and Lifjeld 1988; Wright et al. 1998). Although we didn't measure prey delivery for ctrl females, there was no significant difference in the amount or type of prey brought back to the nest between ctrlRT females and clipRT females. We measured no discernable difference in other foraging metrics (i.e. number of prey and prey type), despite the other well-documented cases in which individuals change their load size or prey type after a clipping treatment. (Leclaire et al. 2011; Weimerskirch et al. 1994.; Wright et al. 1998). In addition, activity measured using automated telemetry did not correlate with any direct measurement of parental care (i.e. provisioning rate, load size, and number of total prey/tipulid larvae delivered to the nest) in our study, suggesting that activity is measuring another component of an individual's behaviour not directly related to chick-rearing. The only correlate of activity we found was with the number of black soldier flies provisioned. Black soldier flies are a novel prey item on our field site, first appearing in 2015 (Gillespie et al. unpublished). Females may be flying further away from the field site to obtain this prey item, which may be why we see the increase in activity.

Some studies have reported future fitness costs of an increased workload during parental care (Daan et al. 1996; Jacobs et al. 2013). Indeed, we found that ctrl females outperformed ctrlRT and clipRT females in second broods and productivity the following year. In addition, there was an additive future fitness consequence of clipRT females. Given that females with a greater workload suffer future fitness costs, along with the observed decrease in body condition in the middle of chick-rearing, our results suggest that females allow for their condition to deteriorate in order to maintain their current reproductive productivity (as seen in the additive effect of clipRT females).

While overall ctrl females had a higher current productivity and future productivity than either treatment group, we found very little additive effect of wing-clipping between the ctrlRT females and clipRT females. Between the two experimentally manipulated groups, there was no difference in provisioning rate, prey type, load size, brood size at fledge, and chick quality. The only major difference between treatments was that clipRT females had a greatly reduced activity while chick-rearing, something we were only able to observe because of automated telemetry. So, clipRT females maintained all foraging metrics that are directed towards parental care, despite the decrease in activity. In addition, while provisioning rate is a good predictor for brood size at fledge, there was no relationship between activity and brood size at fledge. Therefore, activity appears to be measuring a component of behaviour not directly related to parental care. ClipRT females may instead be reducing behaviour associated with self-maintenance, thus explaining the greater decrease in mass while chick-rearing and greater future fitness costs. Although no other study we are aware of has used activity from an ARU system to quantify workload during parental care, we can compare our results to previous studies using daily energy expenditure (DEE) to quantify workload. A meta-analysis by Elliott et al. (2014) concluded that overall, studies that added loads, clipped wings, or attached recorders to chick-rearing birds and then measured DEE, found that DEE did not significantly vary between handicapped and non-handicapped birds. They suggested that handicapped birds either reduced energetic investment in themselves or reduced energetic effort towards rearing offspring to remain below an energetic ceiling. In our study, activity of ctrlRT females was 1.3 X greater than clipRT females, yet there was no significant difference in productivity, chick quality, provisioning rate, load size, and prey type. Thus, clipRT females may be maintaining their delivery of food to their chicks, despite the expected increase in energy expenditure to do so, at a cost towards self-maintenance. So in conclusion, female starlings maintain their foraging effort and current reproductive productivity despite a decrease in foraging efficiency. The decrease in foraging efficiency comes as a cost, and females perhaps have less energy to allocate towards self-maintenance (seen in the decrease in activity) resulting in mass loss and a decrease in future productivity.

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3.6. Tables

Table 3-1. Mean productivity and fledging quality for ctrl, ctrlRT, and clipRT females

		ctrl n = 38	ctrlRT n = 16	clipRT n = 25
Brood Size at Fledge (Including abandonment)	Mean	4.03	2.51	1.35
	SEM	0.29	0.32	0.34
	Range	0-6	0-6	0-6
Brood Size at Fledge	Mean	4.34	3.84	3.38
	SEM	0.24	0.19	0.36
	Range	1-6	2-6	1-6
Fledging Mass (g)	Mean	76.08	73.15	73.68
	SEM	0.82	0.96	1.16
	Range	57.93-89.25	53.54-87.69	52.49-91.93
Fledging Tarsus Length (mm)	Mean	33.28	30.32	30.14
	SEM	0.13	0.27	0.34
	Range	25.52-36.76	25.14-35.49	23.41-34.90
Fledging Wing Chord (mm)	Mean	90.54	88.08	86.55
	SEM	1.44	1.51	1.63
	Range	76-101	74-103	74-100

SEM, standard error of the mean.

Sample size for brood size at fledge (including individuals that abandoned) is as follows; ctrl: 38, ctrlRT: 37, clipRT: 34

3.7. Figures

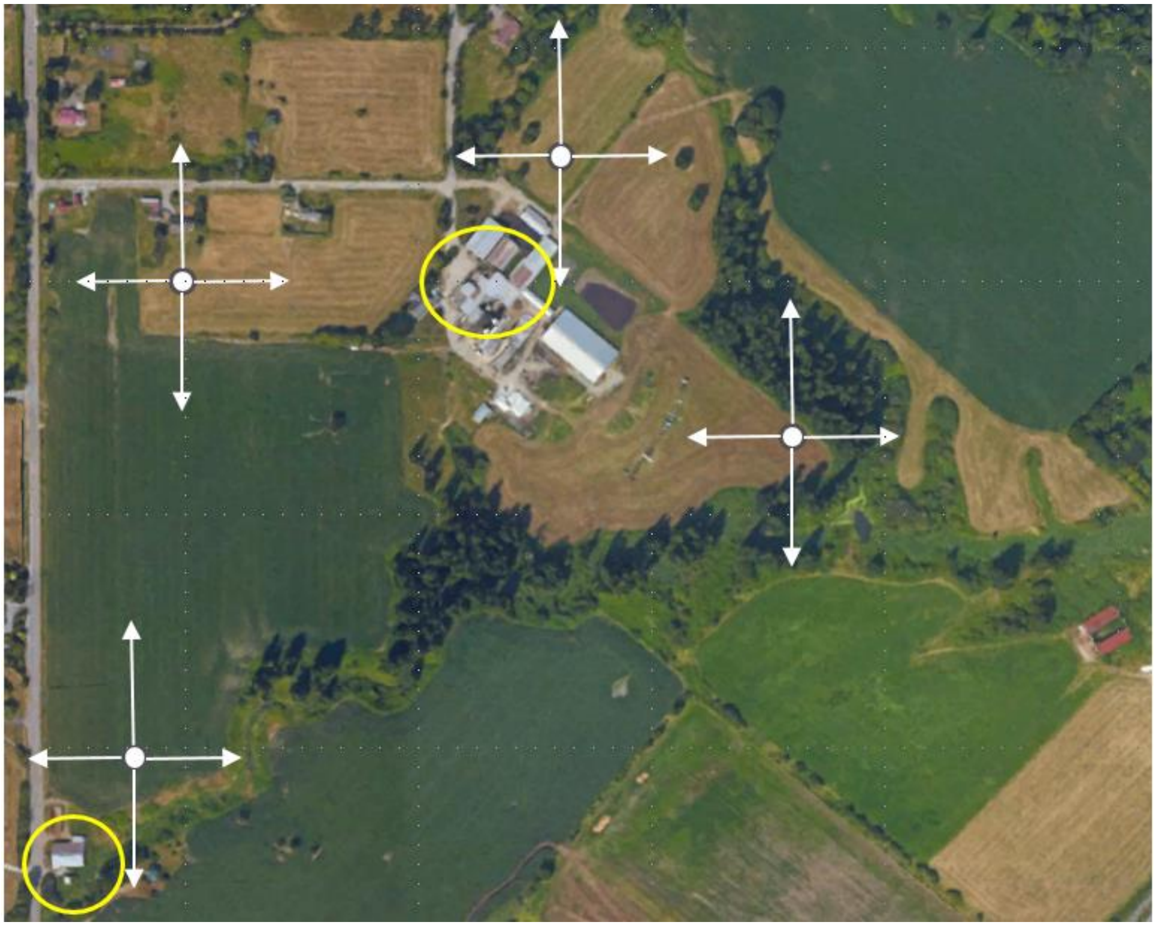

Figure 3-1. **Image from Google Maps of Davidstead Farms. White circles indicate the location of each ARU with arrows specifying the direction of each antenna. Yellow circles designate the location of the nest boxes.**

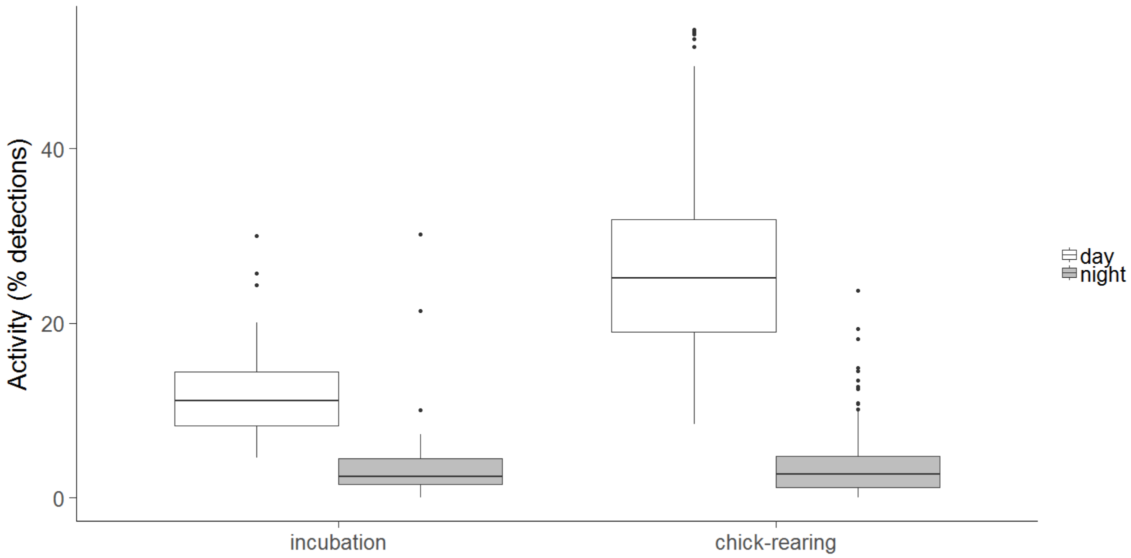

Figure 3-2. Activity for all radioed birds during incubation and chick-rearing (split by day and night)

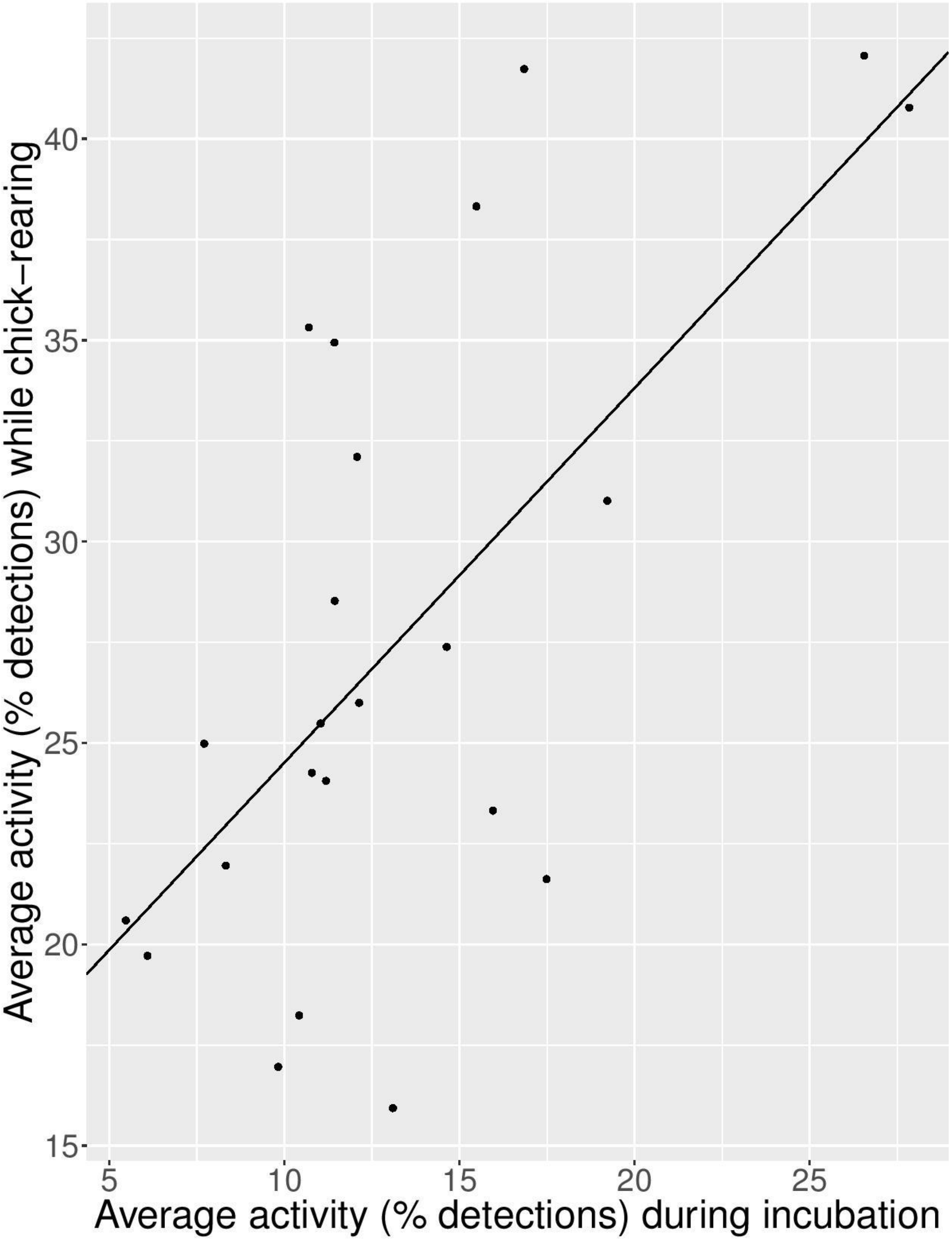

Figure 3-3. **Average activity during incubation predicts average activity during chick-rearing.**

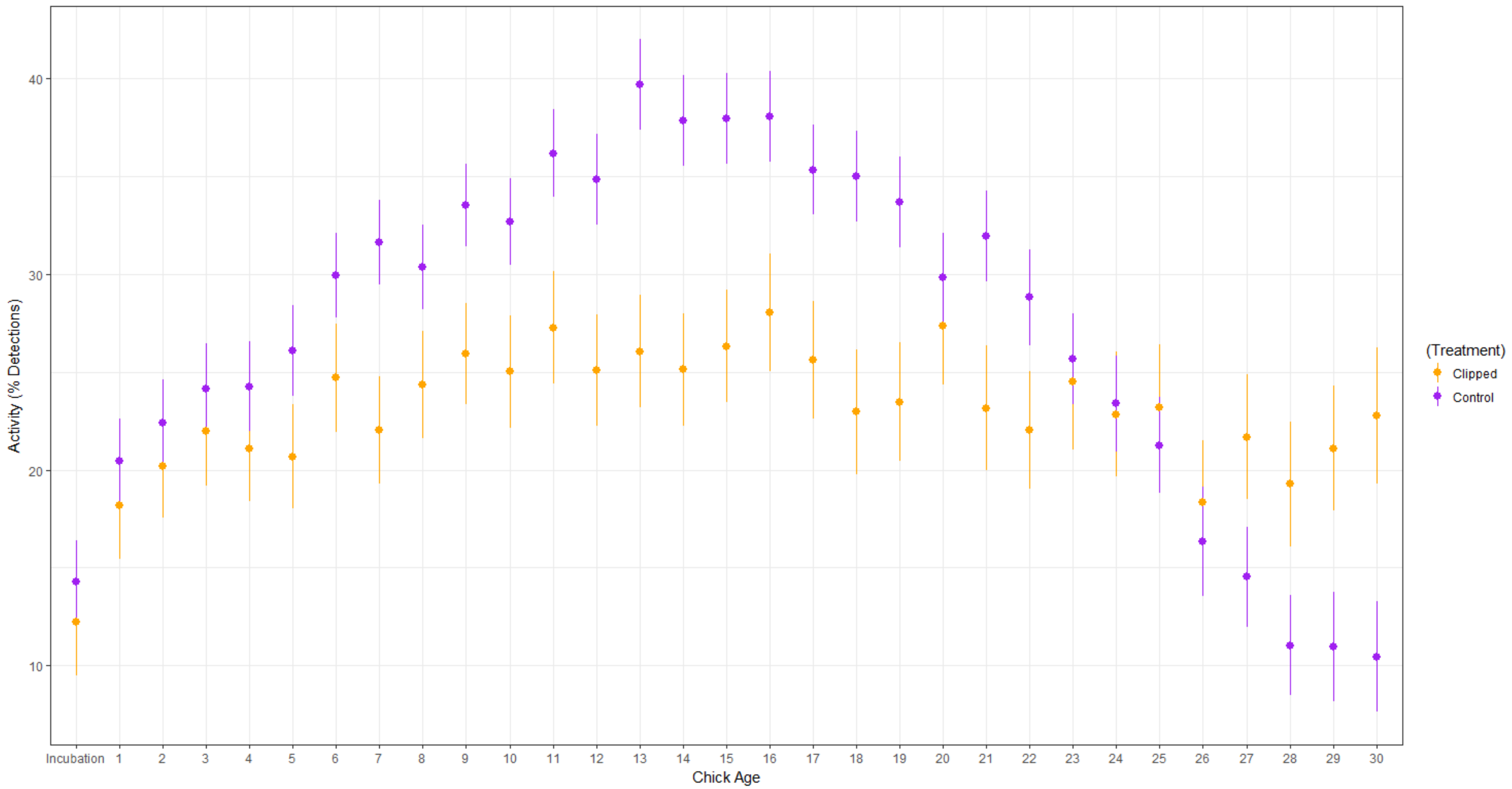

Figure 3-4. **Average activity per day for both ctrlRT individuals and clipRT individuals from incubation to post-fledging. Incubation activity was averaged across days (see text).**

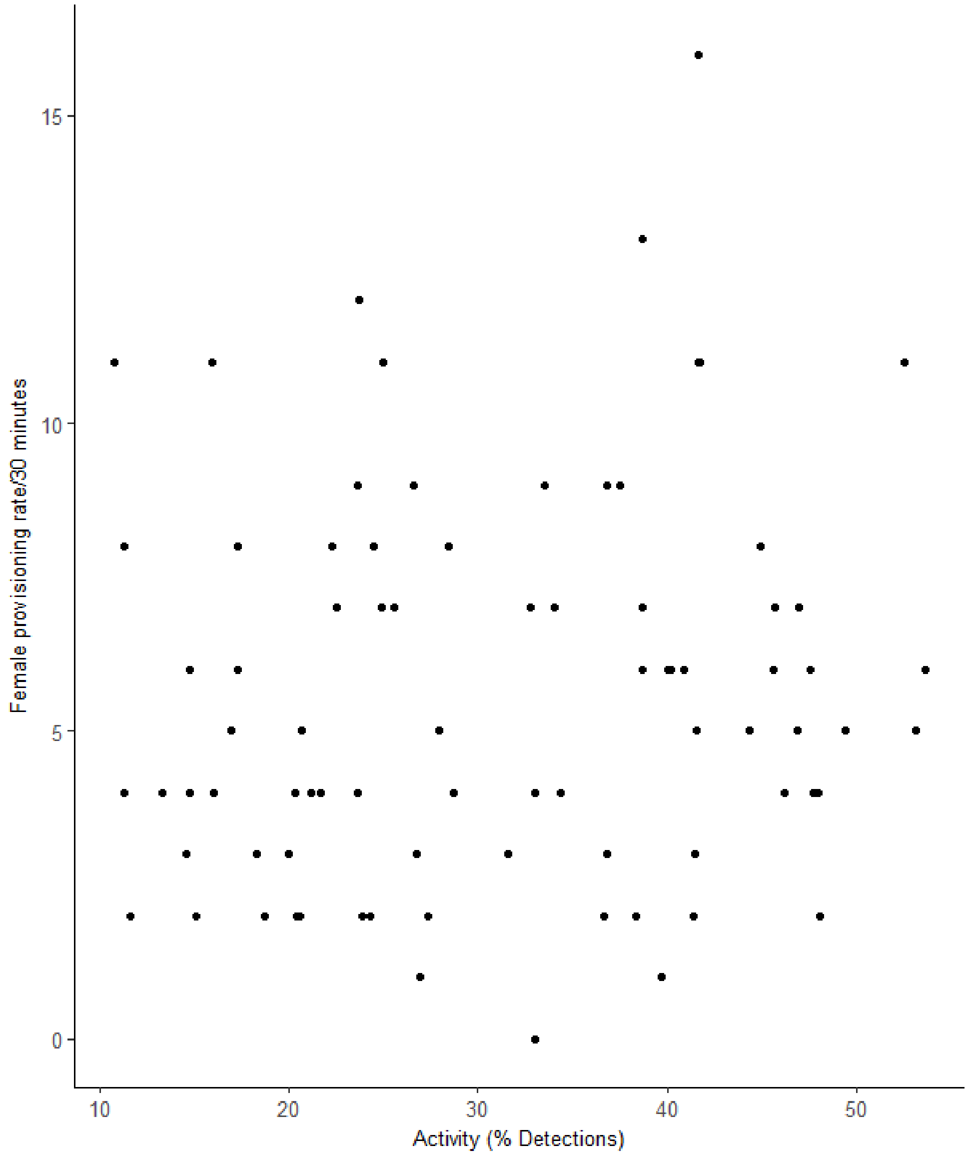

Figure 3-5. **Activity (% active detections) does not predict female provisioning rate**

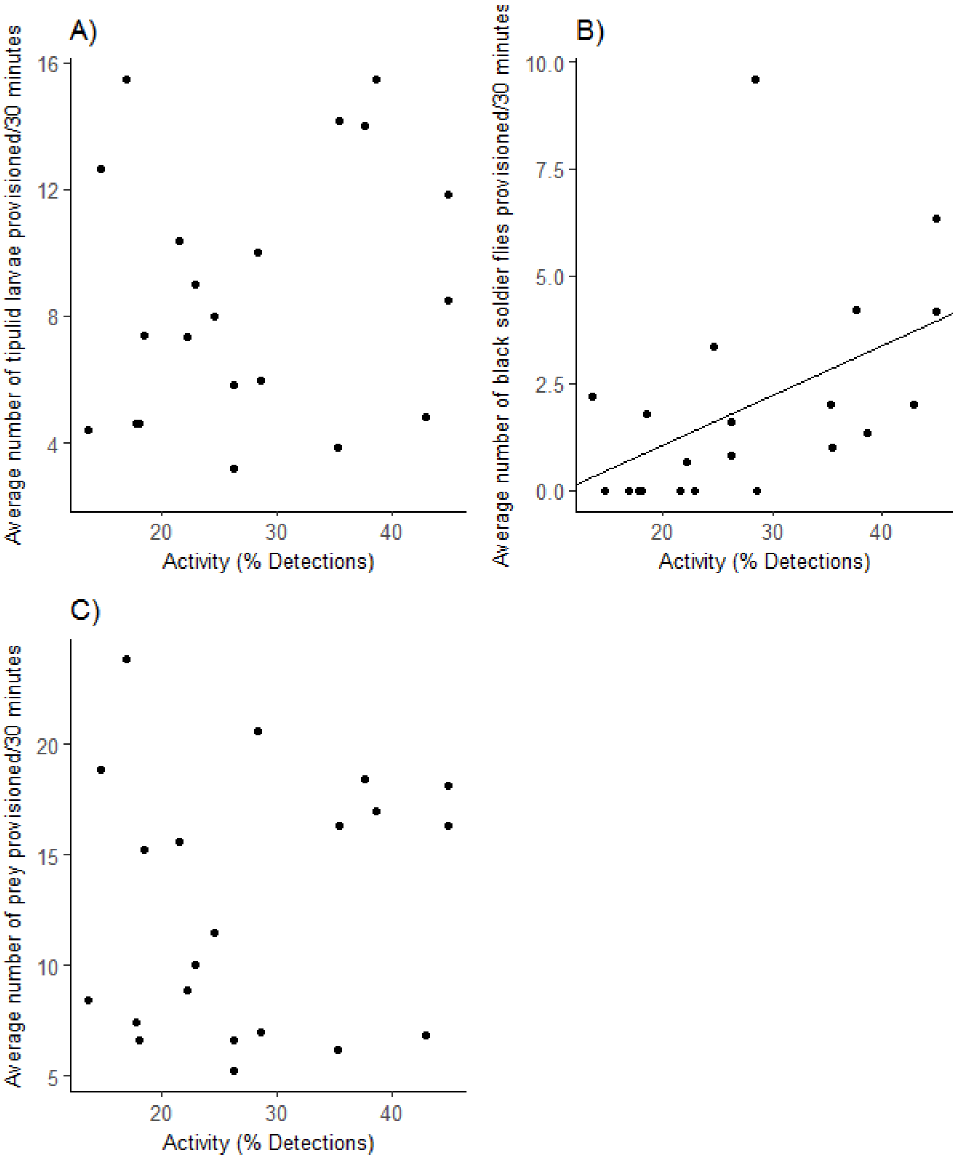

Figure 3-6. **A) Average total activity (% active detections), days 0-21, does not correlate with the average number of tipulid larvae delivered to the nest/30 minutes or C) the average number of prey brought back to the nest/30 minutes. B) Average total activity (% active detections) correlates with the number of black soldier flies brought back to the nest/30 minutes.**

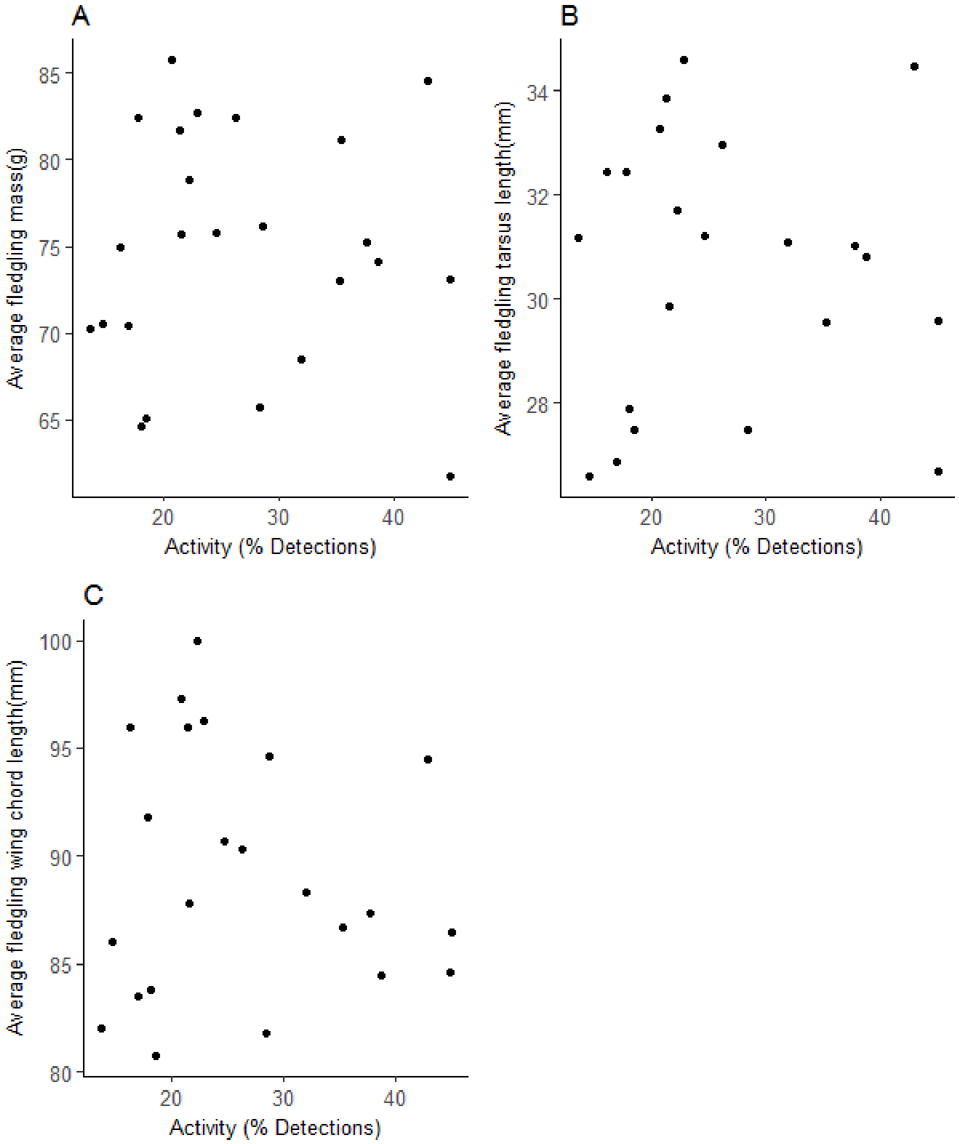

Figure 3-7. **Neither a) fledgling mass (g), b) fledgling tarsus length (mm), nor c) fledgling wing chord length (mm) were correlated with average activity (% active detections) across the chick-rearing stage**

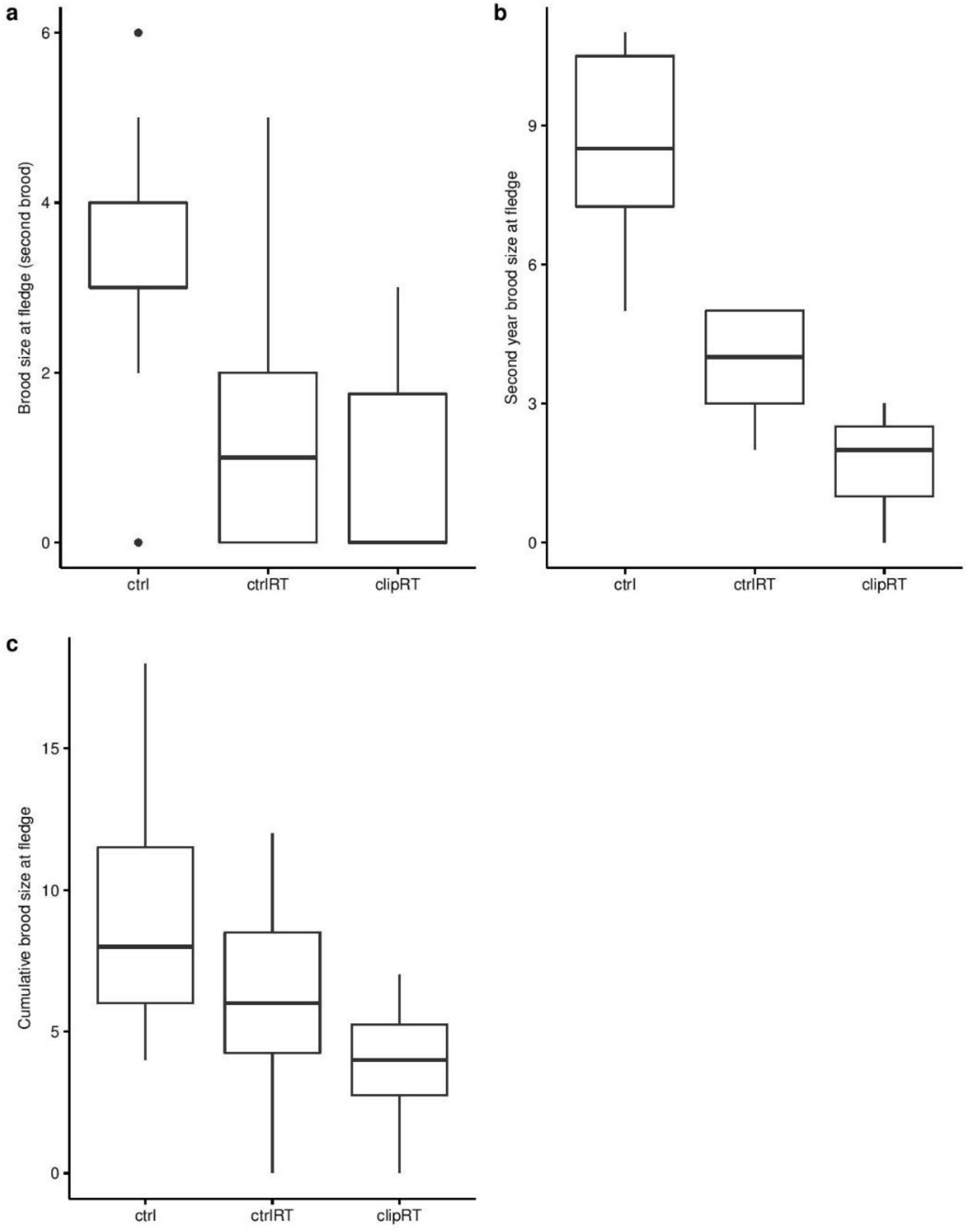

Figure 3-8. **a) Brood size at fledge per treatment for second broods. b) Brood sizes at fledge for all treatments the following year, and c) cumulative brood size at fledge for all treatments (year 1 and year 2). Plots b) and c) only contain data for individuals in 2015.**

Chapter 4.

General Conclusion

In summary, individuals, when subject to an experimentally increased workload, had lower current reproductive investment, current reproduction, and future reproduction and survival (Table 4-1). Females who continued to raise chicks following the manipulation, fledged fewer chicks, but also, suffered a cost in terms of survival and future productivity. Costs of reproduction were even more apparent with the additive effect of wing-clipping. Wing-clipped females not only suffered in terms of the number and size of their offspring in their current reproductive attempt, but also were less likely to initiate a second brood, return the following year, and generally had lower future reproductive productivity. Even so, standard foraging metrics used to quantify workload (provisioning rate, prey type, and number of prey delivered) revealed very little differences between treatment groups. Nevertheless, wing-clipped females had dramatically lower activity during the chick-rearing period suggesting that females maintain their provisioning behaviour at a cost (lower second brood size at fledge, return rate, and cumulative brood size at fledge).

This observed overall trend, however, differed depending on the year (irrespective of our definition of “good” and “bad” years). CtrlRT females, for example, did as well as the ctrl females in 2013/2015, better than ctrl females in 2014, and worse than ctrl females in 2016. We then took a closer look at the foraging behaviour of individual females (2015 and 2016) using a novel automated radio telemetry array. For two groups with no difference in current reproduction (ctrlRT vs. clipRT), there was no difference in the provisioning rate, number of prey, and prey type, and yet activity of clipRT individuals was significantly less than the activity of ctrlRT females. Individuals may be mediating the increased workload by reducing self-maintenance and maintaining their current reproductive bout, explaining the observed results of reduced future productivity and survival.

In general, parents can decide to allocate resources towards their offspring (and compromise future survival) or allocate resources towards future reproduction and survival (resulting in a cost to the chicks). More specifically, individual females may reduce parental care, resulting in a reduction in nestling quality or increased chick mortality (e.g. Mauck and Grubb, 1995). Individual females may also choose to maintain their current reproductive investment at a cost to future survival and reproduction (e.g Daan et al. 1996; Verhulst 1998). Results from experiments that manipulate workload are extremely varied. Following a brood size manipulation, individuals tend to increase their provisioning effort (Nur 1984; Wright et al. 1998). However, feeding rate per chick tends to decrease, resulting in lighter chicks at fledging (Maigret and Murphy 1997; Wright et al. 1998). Brood size manipulations do not always alter the energy expenditure of the parents, and therefore it may be better to directly manipulate energy expenditure of adults directly to measure effect on reproduction (Moreno et al. 1999; Williams and Fowler 2015). The alternative approach to increase workload is wing-clipping or adding weights. However, results from wing-clipping are also equivocal. Some studies found handicapped birds to decrease their own body mass while maintaining their current reproduction (Paredes et al. 2005; Weimerskirch et al. 1995), whereas other studies found that clipped individuals pass the costs to their offspring (Hegemann et al. 2013; Sæther et al.1993). Our results suggest that individuals may both incur costs and pass on costs to their offspring. We found that individuals who continued to raise offspring following an increased workload raised fewer and lesser quality offspring, and suffered future survival and productivity costs.

The life-history of a species is thought to be a major guide towards individual reproductive decision making (Linden and Møller, 1989; Martin, 2004). We should expect responses between species to vary along a gradient. Long-lived species, or species with a higher chance of survival, should pass more costs onto their young on a given reproductive bout and allocate resources towards future survival and fecundity. Short-lived species, with lower adult survival and chance of breeding again, should allocate resources towards current reproduction. A meta-analysis from Santos and Nakagawa (2012), looked at the phylogenetic relationship in trade-offs between parental effort and survival. However, they found that energy allocation towards reproduction and survival is irrespective of the organism's life-history strategy. European starlings are a relatively short lived species so we would expect them to invest more into their current reproductive bout. As expected, following an increased workload, individual females that continued to raise chicks suffered costs in terms of survival and future productivity. Furthermore, geographical variation is thought to alter optimal balance of energy allocation to reproduction and survival (Tieleman et al. 2008). Largely, tropical species have smaller clutches, but higher survival rates than temperate species, so life-history theory predicts tropical birds to invest less in a given reproductive bout than temperate species (Tieleman et al. 2006). Still, comparing results between tropical and temperate species, we find varied results (Tieleman et al. 2008; Wegmann et al. 2015; Winkler and Allen 1995; Young 1996). One possible reason that we find neither phylogenetic nor geographic signals here is due to yearly variability. Our results in chapter 2 suggest that individuals alter their reproductive decisions when faced with an experimental increase in workload, depending on the year. Although individual reproductive decisions were irrespective of our definition of “good” and “bad” years, our results suggest that reproductive decisions can vary yearly.

A meta-analysis by Elliott et al. (2014) determined that overall, studies that added loads, clipped wings, or attached recorders to chick-rearing birds and then measured DEE, found that DEE did not significantly differ between handicapped and non-handicapped birds. They suggested that handicapped birds either reduced energetic investment in themselves or reduced energetic effort towards rearing offspring to remain below an energetic ceiling. Therefore, in many studies (including ours) when handicapped and non-handicapped birds (ctrlRT and clipRT) maintain provisioning rate, load size, and ultimately productivity, they are doing so while expending the same amount of energy. Thus, less energy expenditure goes towards self-maintenance or self-feeding. Future studies should deploy accelerometers to incorporate the energetic costs of specific activities (Wilson et al. 2006). Accelerometers allow for robust measurements of static and dynamic acceleration, and can therefore provide an index of nearly instantaneous energy expenditure by measuring the costs of fine-scale behaviours (e.g. flying, foraging). As reported in chapter 3, clipRT starlings had lower activity than ctrlRT starlings while chick-rearing, despite no difference in provisioning rate, number of prey, pre type, and productivity. Therefore, accelerometers can illuminate whether the same activity (e.g. foraging and flying) is more energetically demanding for clipped individuals.

Furthermore, other studies have used automated radio telemetry to triangulate exact locations of individuals (Ward et al. 2014; Ward et al. 2013). Clipped individuals may be making adjustments in their foraging distance, making shorter trips to accommodate for the increase in flight costs.

4.1. References

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Table 4-1. **The effect of a radio-transmitter and additive effect of wing-clipping on all traits measured across four years.**

	Trait	ctrl	ctrlRT	clipRT
			Increasing workload ⟹	
Current Investment	Abandonment	9%	12%	*49%*
	Mass loss (g)	1.1	2.5	*3.6*
Behaviour	Female Provisioning Rate/30min	5.1	4.4	4.2
	Male Provisioning Rate/30min	1.6	1.2	1.3
	Female tipulid delivery		74%	73%
	Female black soldier fly delivery		14%	15%
	Female rat-tailed maggot delivery		12%	12%
	Male tipulid delivery		75%	74%
	Male black soldier fly delivery		12%	15%
	Male rat-tailed maggot delivery		13%	11%
	Female number of prey delivered/30 min		11.1	12.9
	Male number of prey delivered/30 min		3.9	3.7
	Activity (measuring while chick-rearing)		30.9	22.1
Current Productivity	Brood Size at fledge	3.6	3.1	2.6
	Fledgling mass (g)	75.4	74.0	73.9
	Fledgling tarsus length (mm)	33.3	31.7	31.1
	Fledgling wing chord length (mm)	89.6	88.5	88.5
Future Productivity	Initiation of second brood	57%	56%	37%
	2nd brood size at fledge	1.9	1.3	0.7
	Return rate	37%	41%	30%
	Subsequent year brood size at fledge	1.1	1.2	1.1
	Cumulative brood size at fledge	5.2	5.3	2.7

Appendix.

Automated Radio Telemetry Calibration

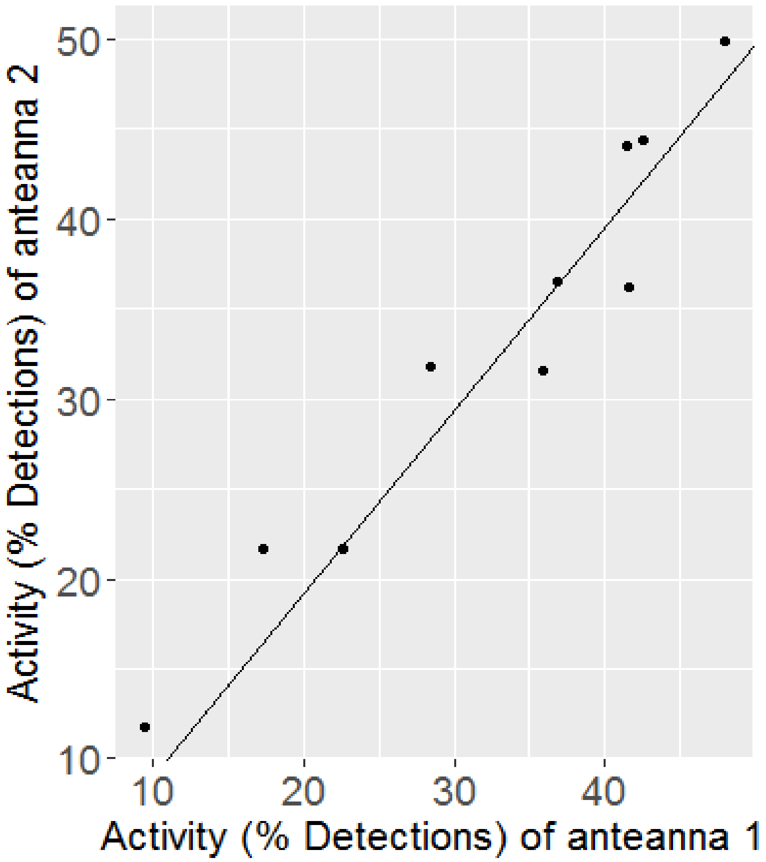

Figure A1. **Activity using one antenna is predicted by the activity of another antenna on the same ARU ($R^2 = 0.92$. $P \leq 0.001$). We used 10 random samples for this analysis.**

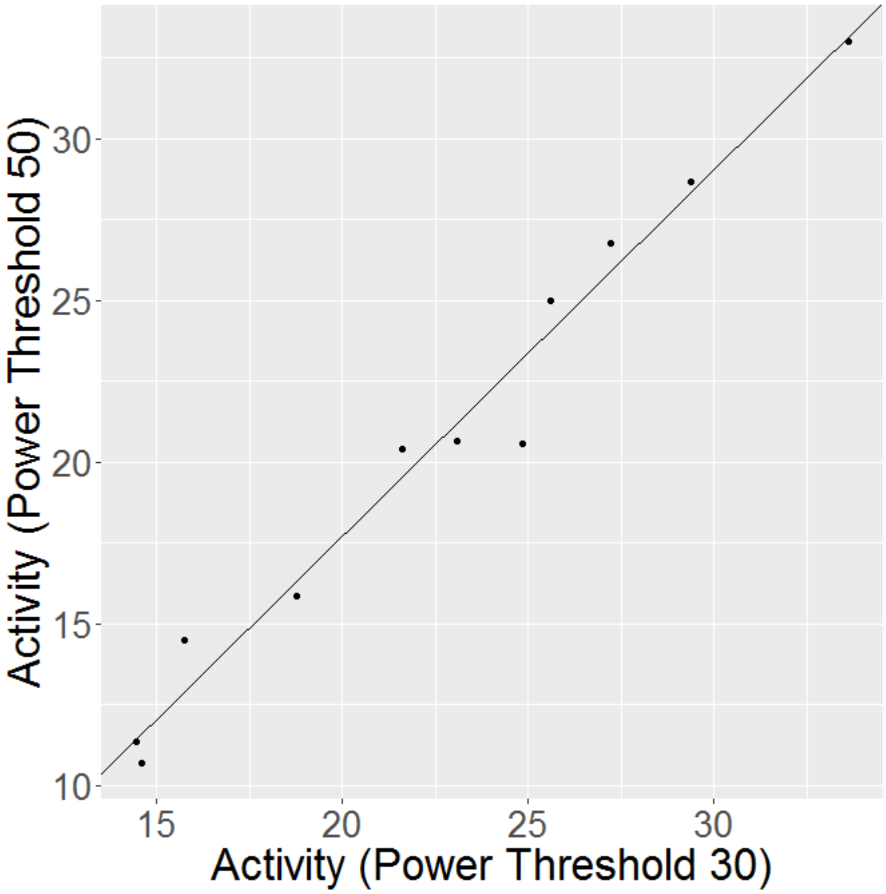

Figure A2. **Activity using a Power threshold of 50 is predicted by activity using a Power threshold of 30. ($R^2 = 0.97$. $P \leq 0.001$). We used 11 random samples for this analysis.**

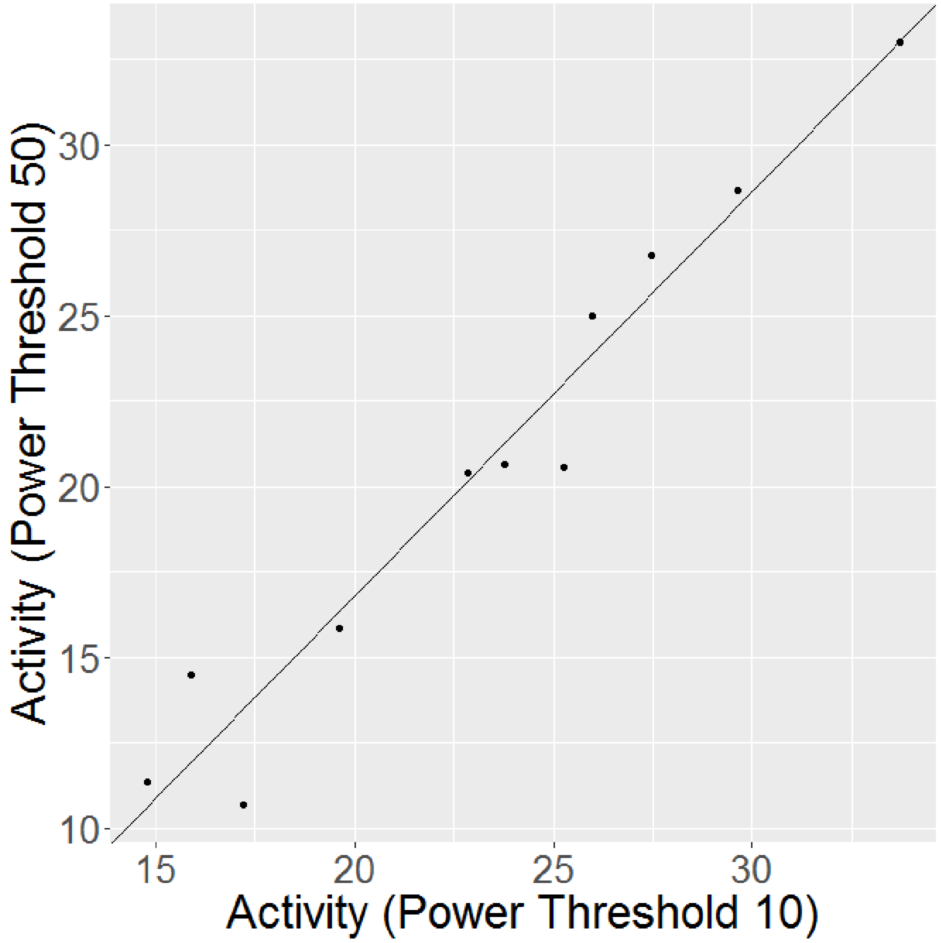

Figure A3. Activity using a Power threshold of 50 is predicted by activity using a Power threshold of 10. ($R^2 = 0.95$. $P \leq 0.001$). We used 11 random samples for this analysis.

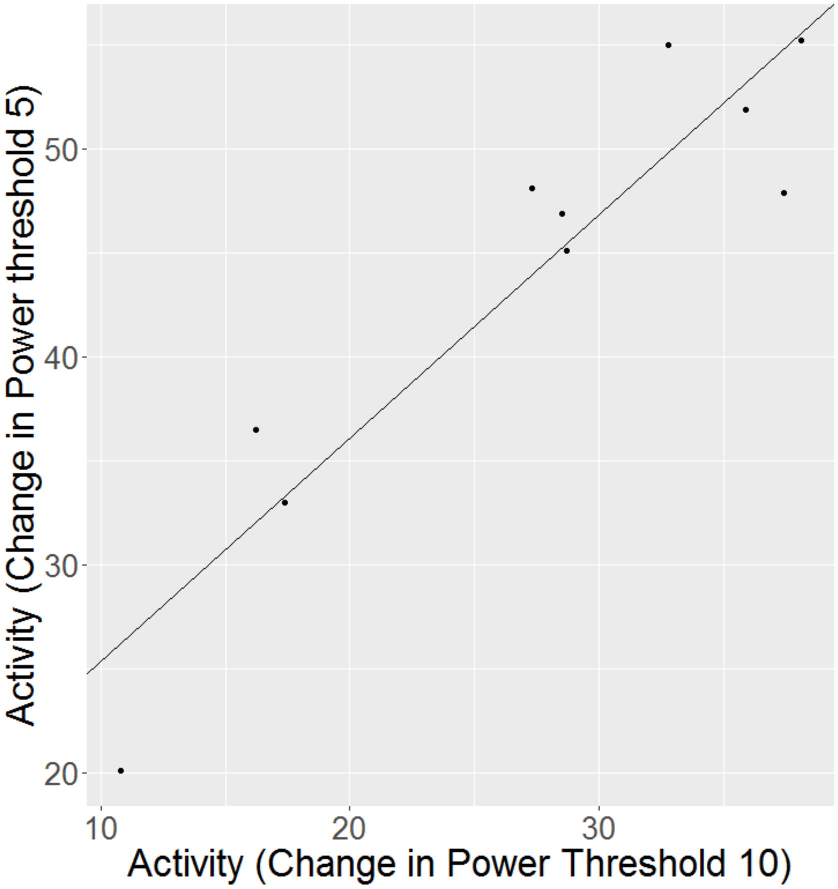

Figure A4. Activity using a change in power threshold of 5 is predicted by activity using a change in Power threshold of 10. ($R^2 = 0.84$. $P \leq 0.001$). We used 10 random samples for this analysis.