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# Fear Of Predators Compromises Parental Care And Juvenile Survival In A Songbird

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A thesis submitted in partial fulfillment of the requirements for the degree in Master of Science

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FEAR OF PREDATORS COMPROMISES PARENTAL CARE AND JUVENILE  
SURVIVAL IN A SONGBIRD

(Thesis format: Integrated Article)

by

Philip (Blair) Medland Dudeck

Graduate Program in Biology

A thesis submitted in partial fulfillment  
of the requirements for the degree of  
Masters of Science

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## **Abstract**

Predators kill, but the risk of being killed is also a powerful force affecting survival because scared prey eat less, thereby increasing the likelihood of starvation. Young of most animals are extremely vulnerable to predators and may alter their behaviour to limit detection. I investigated the previously unexplored effects that predation risk has on the behaviour of newly fledged offspring and their parents, and the impact this has on offspring survival. I manipulated predation risk using sound and found that parent song sparrows reduced their feedings, providing 60% less food overall. Critically, not only did this parental response estimate survival of individual offspring, it allowed me to project that the number of surviving fledglings decreased by ~24%, and fear overall reduced the number of offspring produced per year by ~54%. Counter to my expectation, song sparrow fledglings actually appear to be increasing their auditory detectability in response to reduced provisioning due to their parents' response.

**Keywords:** Perceived predation risk, anti-predator behaviour, anti-predator behaviour costs, parental care, survival, post-fledging, parental provisioning, song sparrow (*Melospiza melodia*)

## **Co-authorship**

Marek C. Allen will be the third co-author on the manuscript to be published from this thesis. Marek was integral in the data collection process, helping to locate the nests of our study species and doing the attaching of the radio transmitters to the sparrows that I conducted my research on.

Dr. Michael Clinchy will be the fourth co-author on the manuscript to be published from this thesis. Mike also played a key role in the design and development phase of this experiment. He helped with the construction of much of the equipment I used during the predation risk manipulation. He also contributed by providing feedback regarding writing, presentations and data analysis.

Dr. Liana Zanette will be the second co-author on the manuscript that is published from this thesis. Liana was central in the development and planning phase of this experiment. Her research expertise and fundamental knowledge of ecology played a key role in helping me accomplish this research. She also helped by providing feedback during data analysis and manuscript preparation. Her NSERC grants also funded my research.

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# Chapter 1

## General Introduction

### 1.1 Predator risk effects on prey populations

Typically, predator effects on prey demography have been attributed to direct killing, limiting prey populations by catching and consuming individuals (reviewed in Pritchard *et al.* 2006). I now understand that predators have additional effects on prey populations, even to the degree that can influence the entire dynamics of an ecosystem (Estes *et al.* 2011). In addition to direct mortality, the fear of predators also elicits physiological, behavioural and morphological responses, and these responses associated with the risk of being killed may alter prey population dynamics (Preisser & Bolnick 2008). Even more striking is the immense number of empirical studies, conducted on a variety of taxa, that argue that predation risk effects may have an equal, if not greater, influence on prey demography than direct predation alone (Preisser *et al.* 2005; Sheriff *et al.* 2009; Zarette *et al.* 2011; Hua *et al.* 2014).

The rate at which a population grows depends on the various components that affect the key demographic parameters of births (i.e. the number of propagules produced) and deaths. There are a myriad of factors that could potentially limit prey populations but two of the most well-studied are food and predators. Researchers face a daunting challenge in determining the population level effects that predation risk may have on prey, as it requires the manipulation of risk in the absence of direct killing. Despite this challenge, a number of studies have begun to measure the effect risk of predation has on prey survival (Creel & Christianson 2008; Sheriff *et al.* 2009; Zarette *et al.* 2011;

Macleod *et al.* 2014). Several microcosm studies using invertebrates have adopted this design with the predators in these model systems being directly manipulated and serving as threatening stimuli without actually being able to harm the prey. Here, direct killing by predators has often been directly eliminated by gluing shut (e.g. Peckarsky *et al.* 1993; Schmitz *et al.* 1997) or partially amputating (e.g. Nelson *et al.* 2004) the mouthparts of predators (e.g. stoneflies, spiders and damselflies). These risky predators (Schmitz *et al.* 1997), which can scare but not kill (Preisser *et al.* 2005), are then introduced to enclosures with prey (e.g. mayfly larvae, grasshoppers, aphids, respectively). Predation risk effects are then measured by comparing prey populations in enclosures with and without predation risk. These experiments demonstrate that risk of predation alone results in decreases in population growth equal to or greater than the effect seen when the predators can kill. Recent manipulations in terrestrial vertebrate systems provide further evidence of the importance of risk effects on prey demography by examining their effects on reproduction. Sherrif *et al.* (2009) reported that pregnant hares that were exposed to a threatening live predator while pregnant gave birth to poorer conditioned offspring and suffered a reduced birth rate. Probably the best example is provided by Zanette *et al.* (2011) who observed an astounding 40% decrease in population growth of a wild song sparrows (*Melospiza melodia*) when they experimentally increased the level of predation risk in the absence of direct nest predation, using predator playback calls and predator exclusion. These studies demonstrate that the effects of perceived risk of predation are costly and must be considered when calculating population level effects that predators have on prey.

## 1.2 Predation risk effects on prey behaviour

While it is clear that the effect of perceived risk of predation has measurable consequences for prey populations, these effects are likely a product of the costs that perceived risk of predation have on prey at the individual level. Prey perceive the ambient risk of predation that is present in the environment they inhabit (reviewed in Caro 2005) and are capable of responding to changes in risk by shifting their behaviour (Schmitz *et al.* 1997; Lima 2009; Wirsing & Ripple 2011). These anti-predator responses do have an inherent cost, as they facilitate critical functional trade-offs that affect survival (Creel and Christianson 2008; Zanette *et al.* 2014).

Predators pose a clear and present challenge to prey survival, forcing individual prey to make choices as a means to minimize their risk of being preyed upon. Prey can adjust their behaviour through a suite of anti-predator responses, such as changes in foraging, habitat use, and vigilance (Lima 1998; Caro 2005; Stankowich & Blumstein 2005), in an effort to improve their probability of survival. There are a large number of published cases covering a diverse range of taxa that demonstrate how prey are sensitive to predators and how these prey employ these sophisticated anti-predator behaviours in response to elevated perceived risk (Lima & Dill 1990; Apfelbach *et al.* 2005). Bray and Nieh (2014) report that honeybees (*Apis mellifera*) avoid foraging at feeders 67% of the time when a live predator such as a mantis (*Tenodera sinensis*), is present. Bees also displayed a 1.8 fold reduction in their foraging recruitment behaviours to conspecifics, suggesting that predator cues can cause a colony-wide shift in foraging behaviour. Similarly, under conditions with high tiger shark (*Galeocerdo cuvier*) densities, dugongs (*Dugong dugon*) change their foraging behaviour by moving to deeper waters, which

represent lower-quality foraging areas than the lush shallow banks that they prefer (Wirsing *et al.* 2007). Further studies have found prey responding to increased levels of predation risk by reducing activity and the size of their home range (Borowski & Owadowska 2010), in addition to increased vigilance (Cassini 1991; Morrison 2011). These studies, along with many others, illustrate the drastic consequences of predator-induced effects on prey behaviour in vertebrates and invertebrates alike (reviewed in Brown & Kotler 2004; Caro 2005; Schmitz *et al.* 2008).

Anti-predator behaviours may reduce the likelihood that prey are killed by predators, but they do carry significant costs. Reducing foraging and increasing vigilance in response to perceived risk can limit the amount of time prey have available to obtain necessary energy reserves (Carey & Moore 1986, Brown *et al.* 1988, Childress & Lung 2003; Trussell *et al.* 2003), although prey can mediate this loss by increasing their feeding intensity (Schmitz 2004). Furthermore, shifting to habitats with lower-quality resources in response to perceived predation risk can result in changes in diet that limit nutrient uptake and energy budgets (Schmitz 2004). For example, elk (*Cervus elaphus*) populations have been shown to switch from foraging in the high-quality open grasslands to the lower quality, but safer, conifer forests following the re-introduction of wolves (*Canis lupus*) into Yellowstone National Park (Creel *et al.* 2005). Therefore, under increasingly dangerous conditions, prey may choose to sacrifice foraging in an effort to reduce their likelihood of encountering predators, or limit their foraging to periods and locations that are safer (MacLeod *et al.* 2007a). As predation risk increases, a prey's ability to acquire adequate nutrition may not be restricted by the absolute quantity of resources available, but rather may result from prey not being able to access food or

expending more energy to obtain those resources (Krebs *et al.* 1995). As prey largely face two sources of mortality, starvation and predation, they have to balance their energy reserves to minimize the risk of death (Lima 1986, McNamara *et al.* 2005). Thus, it is apparent that mortality, caused by starvation and decreased reproductive success, can be attributed to the predator-induced behavioural changes that prey adopt (Boonstra *et al.* 1998, MacLeod *et al.* 2007b).

### **1.3 Parental care effects on populations and offspring survival**

Parental care (e.g. warmth, nutrients, shelter, and protection from predators) is a critical factor in the life history for a wide assortment of taxa extending from mega fauna to invertebrates (Eggert *et al.* 1998; Monteith *et al.* 2012; Lehtinen *et al.* 2014; Maniscalco 2014; Bowen *et al.* 2015). Parental care can be provided to young in a multitude of avenues ranging from nutrients at conception, in the sperm and egg, to parents directly defending offspring from predators (Royle *et al.* 2012). In the perspective of my thesis I will refer to parental care in the context of nutrient provisioning parents provide their offspring. Young are often reliant on their parents for at least the early portion of their lives (Godfray 1991). The quality of parental care offspring receive can vary for a variety of reasons related, in part, to the lifetime reproductive fitness of their parents. This variation in parental care has an inherent cost to the offspring themselves and can critically effect the survival of offspring (Grueebler & Naef-Daenzer 2011).

Royle *et al.* (2012) extensively reviewed the conflict that exists between parents and offspring regarding parental care. An offspring's benefit from care is only limited by the amount of care they receive, particularly with regard to parental provisioning

(Grueebler & Naef-Daenzer 2010; Maniscalco 2014). A conflict between parents and their offspring arises from the offspring's ability to be dishonest about their need for nutrients to parents. Offspring can facilitate feedings from their parents (e.g. begging vocalizations in birds; Mondloch 1995; Budden & Wright 2001; Krauss & Yasukawa 2013; Du *et al.* 2015) even when they are not in need of more food. It has been hypothesized numerous times (Royle *et al.* 2012) that this ability of offspring to lie to their parents could lead to offspring attempting to acquire more food than needed for proper growth and development at the expense of their parents' health and survival.

Parents face reduced reproductive fitness from providing excessive care to fewer young per breeding attempt (Naef-Daenzer *et al.* 2011), as the effort that parents exert on finding food and feeding their offspring can have negative consequences on the survival of parents themselves (reviewed by Godfray 1995; Royle *et al.* 2012). This cost of providing excessive care is exaggerated in animals that reproduce sexually, since parents do not share all of their offspring's genes and therefore do not genetically benefit as much from exerting energy on caring for them (Royle *et al.* 2015). This is especially true for males who cannot be guaranteed complete paternity of all offspring they care for (Gow & Stutchbury 2013). To maximize fitness, parents also should limit their bias to feeding one or two offspring more than other offspring when provisioning multiple offspring at the same time (Smith 1968). By bias provisioning to only portion of their offspring, parents can suffer reproductively due to increased mortality of other young if they unevenly distribute food between or among offspring. This bias in food provisioning among offspring resulting in reproductive loss was illustrated by Naef-Danzer *et al.* (2011), who found that in barn swallows (*Hirundo rustica*), a multiple brooded species of

bird, parents stop taking care of their young at an sub-optimal age post-hatch in order to start their second nest attempt, despite the fact that offspring from first nests benefit significantly from extended parental care. This suggests that parents' overall fitness is increased by fledging two nests instead of one, despite the fact that survival of their offspring appears to be negatively impacted in the first nest from parental care ending at a younger age than individuals fledged from the second nest.

Variation in parental care strongly affects offspring survival, with parents directly controlling their offsprings' nutrient uptake, while these same young develop their own foraging and predator avoidance skills. There are a large number of published cases covering a diverse range of taxa that demonstrate how the quality of parental care can be a significant predictor of offspring survival in dependent and independent young (Eggert *et al.* 1998; Grueebler & Naef-Daenzer 2010; Naef-Daenzer *et al.* 2011; Maniscalco 2014). Eggert *et al.* (1998) demonstrated that in burying beetles (*Nicrophorus vespilloides*), larval growth and offspring survival was drastically reduced when their parents were not present to provide care for them. In barn swallows (*Hirundo rustica*) offspring survival doubles as a result of prolonged care from their parents. Grueebler and Naef-Daenzer (2010) attribute this increase in survival with extended parental care to offspring having more time to develop survival skills related to foraging and predator evasion. Similarly, Maniscalco (2014) found that Steller's sea lion (*Eumetopias jubatus*) mothers that nursed their young more intensely and for longer periods produced more surviving offspring. This increased survival in sea pups is partly attributed to the better physical condition these offspring were in when they are weaned, allowing them to

survive longer periods with low nutrition compared to offspring in poorer condition at weaning (Maniscalco 2014).

The quality of care parents provide their offspring also can be negatively affected by risk of predation (reviewed by Lima 2009). This is well demonstrated in birds with perceived risk of predation near nests causing parents to reduce provisioning to their young (Peluc *et al.* 2008; Eggers *et al.* 2008; Zanette *et al.* 2011; Sofaer *et al.* 2012; Ghalambor *et al.* 2013). When this decrease in feedings occurs over an extended period of time it can lead to broods of reduced mass (Dunn *et al.* 2010; Zanette *et al.* 2011), and a drastic increase in nestling mortality (Zanette *et al.* 2011; Allen *et al.* in preparation).

#### **1.4 Perceived risk of predation effects on avian populations**

Numerous studies have recognised that perceived risk of predation may affect population size in bird and mammal prey species (Lima 1998; Preisser *et al.* 2005; Cresswell 2008), but few have attempted to measure the size of these effects (Sheriff *et al.* 2009; Zanette *et al.* 2011; Christianson & Creel 2015). Better-studied invertebrate and aquatic species differ greatly from terrestrial vertebrates both in the way they detect predators as well as the anti-predator strategies they employ. For example, invertebrate prey are extremely sensitive to chemosensory cues of predators, while terrestrial vertebrates, particularly birds, rely almost exclusively on visual and auditory cues of predators (Sanches *et al.* 2015). Furthermore, inducible defences are remarkably common in invertebrates and aquatic vertebrates such as frogs, but almost non-existent in terrestrial vertebrates (Creel *et al.* 2007). These differences in the way prey from different phyla interact with their predators limit our ability to generalize the findings from studies

on invertebrates and/or aquatic vertebrates to terrestrial vertebrate prey species. Lima (1998) describes the comparative scarcity of experiments exploring the effect of perceived risk of predation on populations of terrestrial species, and vertebrates in particular as the “terrestrial gap.” As a result, the effects of predation risk on terrestrial vertebrate populations, and the proximate mechanism of risk effects (on mortality and/or birth rate) are poorly understood (Lima 1998; Luttbeg & Kerby 2005).

Predation is the primary cause of nest failure for birds (Ricklefs 1969; Husek *et al.* 2012), and therefore direct predation is important to avian demography. However, perceived risk of predation also has a major effect on bird demography through the reduction of egg production (birth rate) and/or hatching and fledging success (death rate) (Zanette *et al.* 2011, Allen *et al.* in preparation). Slagsvold (1982) was among the first to hypothesize that females should reduce their investment in nests when threat of nest predation is high, as a bet-hedging strategy. Skutch (1949) hypothesized that parents with fewer nestlings to feed could visit the nest less often, rendering the nest less conspicuous to predators. In a multi-species comparative study, Ghalambor and Martin (2001) found that birds in the Southern Hemisphere (where the threat of nest predation is higher) laid smaller clutches than birds in the Northern Hemisphere (where the threat of nest predation is lower). Recent studies have demonstrated that birds do in fact respond to experimentally manipulated perceived predation risk, in the same way as they vary when comparing between naturally occurring variations in predation rate (Zanette *et al.* 2011; Hua *et al.* 2014). Overall, effects of perceived risk of predation, during the brood rearing period (i.e. egg laying, incubation and nestling rearing) have been reported to decrease fecundity by 40% per year. These findings demonstrate that the perceived risk of

predation plays a significant role in the reproductive success of avian populations. Despite these impressive findings, perceived risk of predation likely has even greater implications for avian populations, specifically on offspring survival post-fledge.

Four experimental studies have tested the effect of perceived risk of predation has on clutch size (birth rate) in birds. Three of these studies used predator playbacks to threaten nesting Siberian jays (*Perisoreus infaustus*), Song sparrows (*Melospiza melodia*) and Eastern bluebirds (*Sialia sialis*) and observed that females exposed to increased perceived risk of predation laid significantly fewer eggs than did control females (Eggers *et al.* 2006; Zanette *et al.* 2011, Hua *et al.* 2014). Fontaine and Martin (2006), in contrast, manipulated threat by removing all potential nest predators, in a multi-species study, but did not find an effect on the number of eggs laid in the first nest. These conflicting results may be due to differences in the means used to manipulate threat or the life history of the focal species (single- or multi-brooded). It is important to note that two of these seminal studies (Eggers *et al.* 2008 and Fontaine & Martin 2006) experimentally manipulated threat, but did not actively eliminate direct predation as was done in the classic studies on invertebrates discussed previously (Schmitz *et al.* 1997; Nelson *et al.* 2004). The findings of Zanette *et al.* (2011) and Hua *et al.* (2014) are more credible, having closely mimicked the design of the original invertebrate studies (i.e. manipulated perceived risk while eliminating direct killing) and therefore reflect the dynamics of terrestrial vertebrates with regard to perceived risk of predation alone.

Perceived predation risk can also affect bird populations by influencing nest concealment. Several authors have shown that females will build nests that are more concealed in vegetation when predation threat is high (reviewed in Lima 2009). This

increased concealment while decreasing the probability of being found comes at a cost, as it has been linked in some cases to colder nest microclimate, which reduces hatch success and nestling condition, thereby affecting reducing offspring production (Marzluff 1988; Eggers *et al.* 2008; Zanette *et al.* 2011).

Duncan-Rastogi *et al.* (2006) showed that activity at a nest is linked to an increased threat of predation in song sparrows (*Melospiza melodia*): nests with higher nest visitation rates were more likely to be preyed upon. Thus, when the threat of predation is high, parents should reduce the rate at which they visit their nests to feed their offspring. If provisioning rates are reduced, nestlings may face starvation. This is exactly what several studies have documented, with reduced parental provisioning rates in response to both short and long term increases in perceived risk of predation (Eggers *et al.* 2008; Fontaine & Martin 2006; Peluc *et al.* 2008; Zanette *et al.* 2011; Ghalambor *et al.* 2013). However, only Zanette *et al.* (2011) directly assessed the relationship between nestling mortality and reduced provisioning rates. They found that under increased perceived risk of predation, and in the absence of direct predation, parents significantly reduced provisioning to their young, nestling mass was lower, and this decrease in mass was positively correlated with the reduction in provisioning. Further, Zanette *et al.* (2011) found that these same offspring died in greater numbers, when exposed to increased risk, and that this was attributed to their poor condition. This effect, in addition to decreases in eggs laid and reduced hatching success due to increased perceived risk, resulted in a 40% reduction in the number of offspring a female produced per year (Zanette *et al.* 2011). Hua *et al.* (2014) found similar but less dramatic effects on seasonal fecundity in Eastern bluebirds (*Sialia sialis*).

Despite how dramatic the described effects perceived risk of predation on avian demography are, it is likely that these effects are not limited to the in-nest period. The young of many bird species receive care from their parents after leaving the nest, these dependent fledglings continue to be fed by their parents for several weeks until they are capable of finding food on their own (reviewed by Cox *et al.* 2014). Zanette *et al.* (2011) hypothesized that perceived risk of predation may have an even greater effect on prey population growth due to effects on dependent juvenile survival mediated by the same factors (i.e. decreased provisioning and subsequent effects on offspring condition) reported during the in-nest stage. In spite of how important this component could be to understanding the total effect that predators have on prey populations, no one has attempted to examine or measure these potential effects (reviewed by Cox *et al.* 2014).

The effects of perceived predation risk on fledgling behaviour also could affect avian populations. Magrath *et al.* (2007) reported that nestlings are capable of recognizing and responding to risk of predation (i.e. decreased their detectability when exposed to the sound of a predator near their nest). If this holds true for dependent post-fledge offspring, where they too reduce their detectability through decreased vocalization, this could in turn further lead to reduced provisioning, in addition to the reduction due to threat of predation perceived by their parents. If this is the case, then fledgling birds may be exposed to even greater decreases to nutrition and thereby incur greater negative effects on their survival. As with many factors associated with the post-fledging period no experiment has tested for this effect on dependent fledgling behaviour.

## 1.5 Research objectives and hypothesis

Breeding birds use several tactics to reduce the threat of predation to their offspring. Even though anti-predator strategies may be successful in reducing losses to direct nest predation, offspring survival is likely to be negatively affected when predation risk is high. Annual offspring production is a cumulative function of birth rate (clutch size) and death rate of young (hatch and fledge success) over an entire breeding season. Studies have indicated that each of these components can be affected by perceived threat of predation (Zanette *et al.* 2011). However, there is a distinct lack of experiments examining the effects of predation risk once the young leave the nest, and no one has examined whether fledglings themselves can recognize or respond to predation risk in their environment.

In Chapter 2, I address how experimentally increasing the level of perceived predation risk in the environment influences song sparrow (*M. melodia*) parental care to offspring during the post-fledging period and how these parental responses affect juvenile survival. Additionally, I will examine how offspring themselves perceive and respond to predation risk in their environments in song sparrow (*Melospiza melodia*). I hypothesize that in response to increased perceived risk of predation, parents will reduce provisioning and this will negatively affect their offsprings' survival. With regard to the fledglings themselves I hypothesize that fledglings should modify their behaviours to reduce their detectability to predators under increased perceived risk of predation. In Chapter 3, I discuss the broader biological significance of my findings and how they can be incorporated into our understanding of the effect of risk of predation on prey demography. As predation risk alone has clear overarching impacts on prey populations

and ecosystems, I also suggest several components of predation risk effects, behaviours, and demography that deserve further attention.

## 1.6 Study species

Song sparrows are one of the most widespread species of bird found in North America, breeding from coast to coast in both the United States and Canada, and as far south as central Mexico. Most of the northern populations are migratory; however, this is not the case with those found along the entirety of the Pacific Coast. In this portion of their range sparrows occupy and defend territories year round (all general life history of sparrows here is reviewed in Arcese *et al.* 2002). Song sparrows are small passerines (approximately 23 g), with mass varying across their range and by sex (12 to 53g, male > female). The species is sexually monomorphic in plumage, and is characterized by its melodious song and distinct brown and beige-streaked breast with its central breast spot, with geographic variation in plumage. Song sparrows inhabit a wide variety of habitat types including forests, shrub land and riparian zones close to fresh or salt water. Like most sparrows they are predominantly insectivorous, but seeds and fruits also make up a large portion of their diet when they are available.

Males of the species establish territories early in the breeding season and attract females through singing. Pairs are socially monogamous and tend to cooperate to defend the territory together for the entire breeding season. Females, alone, construct open-cup nests of leaves and grasses in low-lying vegetation, taking three or more days to complete before laying one egg per day until the clutch is complete (usually 2-4). Females begin incubating the clutch the day the penultimate egg is laid, and the incubation lasts for 13

days at which point the nestlings hatch. Song sparrow nestlings require frequent brooding from the female until they develop endothermy at 5 days post-hatch (Sogge *et al.* 1991). Song sparrow young are altricial, requiring provisioning by parents from the time they hatch until they can feed themselves, typically three weeks after fledgling (Dybala 2013). Song sparrows never re-use nests following fledging or failure. Instead, females build new nests for each attempt, and have been reported to make up to eight nesting attempts per season (Arcese *et al.* 1992).

The population of song sparrows I studied is resident on several islands in the Gulf Islands National Park Reserve, B.C., Canada. This population is resident year-round, and typically has a breeding season that starts in March and ends in August. Predation rate of nests in this population ranges from 48 to 69% across years, with the primary predators being raccoons (*Procyon lotor*), mink (*Mustela vison*), as well as Common ravens and Northwestern crows (*Corvus corax* and *Corvus caurinus*, respectively; Zquette *et al.* 2006).

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## Chapter 2

### Fear of predators compromises parental care and the survival of post-fledged young

#### 2.1 Introduction

Traditionally, predators have been viewed simply as killers, restricting prey populations by catching and consuming individuals (reviewed in Pritchard *et al.* 2006). However, a growing body of research suggests that predators also have strong non-consumptive effects on prey populations wherein the mere risk of being preyed upon (i.e. ‘fear’) can have significant negative effects on prey demography (Brown *et al.* 2001, Creel & Christianson 2008; Creel & Christianson 2010; Zanette *et al.* 2011; Creel *et al.* 2011; Creel *et al.* 2014; Zanette *et al.* 2014). These changes occur through various avenues including altered habitat selection (Kotler *et al.* 1991; Sih 1997), and increased vigilance (Brown & Kotler 2004; Creel *et al.* 2014; Jayne *et al.* 2015). These anti-predator responses can have significant negative effects on prey through decreased feeding rates (Kolster *et al.* 1991; Brown and Kotler 2004) or altered diet (Schmitz *et al.* 1997; Christianson & Creel 2010). These non-consumptive effects of predators on behaviour can have significant costs leading to reduced birth rate and increased deaths, potentially affecting long-term population viability (Relyea & Werner 1999; Sheriff *et al.* 2009; Zanette *et al.* 2011; 2013). Zanette *et al.* (2011) experimentally demonstrated that increased perceived risk of predation significantly reduced the parental care adult song sparrows (*Melospiza melodia*) provided to their young at the nest. This reduction in parental care resulted in offspring with lower body mass as well as increased mortality.

Overall the effect of perceived risk led to a 22% decrease in nestling survival and an overall 40% decrease in the number of offspring produced per year during the in-nest stage. This effect on population growth is likely an underestimate of the total effect that fear of predators alone can have on prey populations if fear causes further losses through reduced parental care after young leave the nest as fledglings (Zanette *et al.* 2011).

Parental care (warmth, nutrients, shelter and protection from predators) is a critical component in the life history of a wide variety of taxa (Eggert *et al.* 1998; Monteith *et al.* 2012; Lehtinen *et al.* 2014; Maniscalco 2014; Bowen *et al.* 2015). Songbirds produce altricial young that are completely dependent on parental care while in the nest and for a period of two to three weeks after leaving it i.e. fledging (Ogden & Stutchbury 1997; Monteith *et al.* 2012; Dybala *et al.* 2013). Consequently, quality of parental care can be a significant predictor of offspring survival in animals that produce dependent young. For example, in barn swallows (*Hirundo rustica*) and Steller's sea lion (*Eumetopias jubatus*), offspring survival was enhanced when the length and intensity of parental food provisioning was increased, respectively (Grueebler & Naef-Daenzer 2010; Maniscalco 2014). Predation risk itself can have significant negative effects on the quality of care parents provide (Karels *et al.* 2000; Eggers *et al.* 2008; Zanette *et al.* 2011; for review see Lima. 2009). With regard to birds, perceived risk of predation near the nest can cause parents to reduce the rate at which they provide food to their nestlings (Peluc *et al.* 2008; Eggers *et al.* 2008; Zanette *et al.* 2011; Sofaer *et al.* 2012; Ghalambor *et al.* 2013). When this decrease in feedings occurs over an extended period of time it can have negative physical effects on the young, such as reduced body mass (Dunn *et al.* 2010; Zanette *et al.* 2011). Offspring mass on its own has been shown to be predictive of

survival (Eggert *et al.* 1998, Krist. 2011, Bowen *et al.* 2015). Zquette *et al.* (2011) found a significant correlation between reductions in feed visits to nestlings and nestling mortality. The authors suggest that the reduction in offspring mass, as a result of reduced feedings, was a significant mechanism that led to the decrease in nestling survival in environments with high predation risk. It is likely that a similar relationship is present after the offspring leave the nest wherein parents that reduce feedings in response to predator cue will have lighter offspring and that they will be more likely to die.

Parental care during the dependent juvenile stage is an understudied yet significant component of the life history of birds particularly with regard to offspring survival (Grueebler & Naef-Daenzer 2010; Tarwater & Brawn 2010). During the first few weeks after leaving the nest, juveniles are likely to face a high risk of mortality because they have not fully developed critical survival skills, such as predator evasion and foraging (reviewed by Cox *et al.* 2014). Parental care during this time is crucial in mediating these risks because the young remain primarily dependent on parents for nutrition (Dybala *et al.* 2013). Despite a considerable focus in the literature on effects of predation risk on parental care, this research has been limited to the nestling phase, with no studies to my knowledge examining predation risk once offspring leave the nest. In fact, very little is known in general about what happens to young birds once they leave the nest, other than that mortality is high (reviewed by Cox *et al.* 2014). This is particularly relevant for conservation and management of species. Researchers interested in tracking the demography of a species require accurate data on the survival at each stage of the animal's life history in order to calculate population survival and growth rates.

Offspring behaviour may also be affected by perceived risk of predation (Magrath *et al.* 2007). Offspring produce begging vocalizations to indicate their need for food and elicit parental care, but changes in such behaviour could negatively affect their survival either through increased predation rates or, alternatively, through increased susceptibility to starvation (Mondloch 1995; Budden & Wright 2001; Krauss & Yasukawa 2013; Du *et al.* 2015). Increased begging behaviour, due to hunger, can make offspring more conspicuous to predators and thereby more susceptible to being preyed upon (Ibanez-Alamo *et al.* 2012). For example, during the nestling stage broods of nestlings that produced more begging vocalizations are more likely to be preyed upon than less vocal broods (Haff & Magrath 2011; Ibanez-Alamo *et al.* 2012). Offspring can perceive predation risk and modify their behaviour accordingly (i.e. become more risk-averse) to reduce their chances of being preyed upon (Magrath *et al.* 2007; Haff & Magrath 2010). For example, in response to a threat near the nest, nestling white-browed scrubwrens (*Sericornis frontalis*) reduce their vocalizations and movement, presumably to avoid being detected by a nearby predator (Magrath *et al.* 2007; Haff & Magrath 2010). Such a response could alternatively lead to a reduction in parental provisioning and thereby expose these offspring to an increased likelihood of starvation.

As fledglings produce the majority of their begging vocalizations when parents arrive with food (Smith 1978), it is important to examine begging behaviour by separating the vocalizations by whether they occurred when the parent was present or absent. To decrease detection by predators, fledglings should only produce excessive begging vocalizations when a parent visits them with food. Begging with a parent present or in close proximity to the fledgling should incur less risk than begging with no parent

present (Leonard & Horn 2001). With a parent present, the fledglings' vocalizations should direct the parent to them and promote feedings. In contrast, begging in the absence of a parent should be inherently dangerous, as it is unlikely to encourage feedings if the parent cannot hear the calls and would instead act as an advertisement to any nearby predators (Haskell 1994; Ibanez-Alamo *et al.* 2012).

Based on the response nestlings have demonstrated when exposed to perceived risk of predation described by Magrath *et al.* (2007), I hypothesized that fledglings may also be able to detect and respond to predation risk through risk-averse behaviours, potentially decreasing their vocalizations to become less conspicuous. If fledglings alter their begging behaviour (i.e. begging less) to avoid predators, they may become more susceptible to starvation since fledglings need to maintain high begging rates to solicit food from parents (Mondocho 1995; Krauss & Yasukawa 2013; Du *et al.* 2015). Conversely, I expected that fledglings that produce more begging vocalizations when their parents are absent even during periods of high perceived predation risk would be responding to need for food rather than perceived risk and increasing their likelihood of detection. Fledglings should also decrease their visual detectability to avian predators, many of which rely heavily on visual cues to detect their prey. Fledglings are highly susceptible to predation largely due to limited mobility particularly soon after leaving the nest (Dybale *et al.* 2013). If they do not recognize the threat that predators pose and respond accordingly (i.e. produces fewer begging vocalizations, hide in cover or stay still to reduce visual detection) they may be exposed to higher predation rates.

In this study, I used playbacks of predator sounds to test the effects of perceived predation risk on parental care and on fledgling behaviour in free-living populations of

song sparrows (*Melospiza melodia*). To expand on the findings of Zanette *et al.* (2011) during the in-nest phase, I examined if these potential changes in parental behaviour are predictive of the survival of fledglings (post-fledge stage) by measuring the number of times parents visits their young to feed them. Parents could compensate for reduced food provisioning visits by feeding their fledglings more at each visit, leading to no differences in overall food intake. To account for this, I also assess parental care as feeding at each visit. I predicted that song sparrows exposed to playbacks of predator sounds would decrease provisioning rates to offspring. I predicted that parents that reduced feeding visits would be more likely to produce offspring that are of inferior physical condition compared to those of parents that did not attenuate their feeding visits. This potential negative effect on offspring condition is likely to lead to higher rates of mortality as a result of both an increased chance of starvation due to reduced nutrition and as well as being preyed upon due to reduced ability to escape. Lastly, I predicted that fledgling song sparrows would respond to predator sounds by decreasing their detectability.

## **2.2 Methods**

### *2.2.1 Study site and species*

I conducted short term (60 min) predator playback manipulations on free-living, banded populations of song sparrows situated in the Southern Gulf Islands National Park Reserve, British Columbia, Canada (48°43'21" N, 123°22'26" W). These manipulations were conducted in order to determine the effects of perceived predation risk on parental care and the possible consequences this had on fledgling survival. The study populations are located at 12 sites over four coastal islands, each < 200 ha in size. Song sparrows in

this region are non-migratory (Zanette et al. 2006b); first clutches are generally laid in early-to-mid April and individual females can have up to three successful nesting attempts per year (Zanette *et al.* 2006a, b). The nesting cycle typically lasts 55 days, consisting of 13 days of incubation followed by 10 to 12 days of brood-rearing prior to fledging. Fledglings are unable to maintain sustained flight for the first week post-fledge and are dependent on their parents for food and protection for the first three weeks (Dybala *et al.* 2013).

I found song sparrow nests by observing females on each territory and following them back to their nest. I banded each nestling with a unique combination of 4 colour bands on day 6 post-hatch and weighed them using a digital pesola scale (accurate to 0.01 g). I equipped two nestlings per nest with light weight (0.35 g) radio transmitters (Picopip A g317, Biotrack, Wareham, UK), see Rappole and Tipton (1991) for details on attachment. To determine which nestlings would receive radios, and to avoid the possible bias related to observing only the largest or smallest fledglings, I ranked all nestlings in a given nest according to their mass, at day 6 post-hatch, and then used this to choose the individuals from each nest that would be equipped. I systematically rotated from nest to nest, first selecting the largest and smallest nestling, then the largest and second largest in the next nest sampled etc. I then monitored nests until they were deemed to have successfully fledged, which was verified through the use of radio-tracking upon finding an empty nest. I then tracked and hand-captured fledglings on the day they left the nest for measurements of body mass. All radio equipped fledglings were from then on radio tracked every second day until the end of the field season, August 31, to determine their

fate as alive or dead based on visual confirmation of the individual's combination of colour bands or by collecting the remains of the individual.

I manipulated the perceived risk of predation using 60 min auditory playback treatments, following methods adapted from Peluc *et al.* (2008). During each of these treatments I observed post-fledging behaviour of 44 family units, family units consisted of one fledgling and the parent or parents that cared for it, and recorded survival data on the same 44 individual offspring. Of these individuals 30 were produced from their parents first nest and 14 from the second nest their parents had produced that year. The majority of fledglings from second nests (9/14) were produced by parents who had failed to fledge young on their first attempt, with all failures due to non-predator related factors. The remaining 5 fledglings, from second nests, did have parents who had produced fledglings from their first nests and were previously exposed to my treatments. To insure I did not bias my data by only observing food provisioning to the largest or smallest fledglings, I used a system similar to how I decided which nestlings would get radios described above, to determine the fledgling who I would observe (i.e. the focal fledgling). Once again I used the rank of the fledgling based on its mass to systematically rotating through from largest to smallest (i.e. selecting the largest in the first nest then the second largest in the next nest and so on). Due to the fact that so few nests fledged 3 fledglings I combined fledglings ranked 3<sup>rd</sup> (8) in mass with those ranked 2<sup>nd</sup> (14) I combined them for a total of 22, compared to 22 first ranked fledglings. I observed these same fledglings a mean of 2.7 day ( $\pm 0.15$ ) after leaving the nest. This age helped account for the very high mortality during the first week post-fledge reported for song sparrows (Dybala *et al.* 2013).

### 2.2.2 Predation risk playback manipulation

All playback treatment manipulations were broadcast between 0600 h and 1500 h, since parental feeding rates decrease outside of this time period (Smith 1978). I broadcast both predator and non-predator sounds for 60 min each, to each of the 44 family units. Both treatments were presented on the same day with a 15 min period of silence between the two treatments. Of the 44 family units I tested, 19, 14 in the first nest and 5 in the second, were presented with the predator treatment first, while the remaining 25, 16 in the first nest and 9 in the second, were exposed to the non-predator first. I located the focal fledgling using radio-telemetry and then set up an array of three portable speakers (Ecoextream, ECOEXGEAR Ltd. Canada), equipped with MP3 players (Hipstreet, 4gb Clip MP3 Player), assembled in a triangle around the individual, with each playback placed 8 m from the fledgling (following methods adapted from Peluc *et al.* 2008 and Gahlambor *et al.* 2013). If the fledglings ever moved further than 8 m from the nearest playback unit, I repositioned the playbacks so that the fledgling was once again at the centre of the triangle, though this only happened in five of the 44 treatments, three in the non-predator and two in the predator. With this design the fledglings could move around within an area of 440 m<sup>2</sup> and still be exposed to the treatment. Song sparrows occupied territories averaging 4000 m<sup>2</sup> so the treatments always stayed within a single territory and the parents and fledglings were not spatially limited by the treatments either.

The playback sounds consisted of calls of four avian predators (common raven (*Corvus corax*), Cooper's hawk (*Accipiter cooperii*), merlin (*Falco columbarius*), sharp-shinned hawk (*Accipiter striatus*)) or four non-predator species (Canada goose (*Branta canadensis*), northern flicker (*Colaptes auratus*), black oystercatcher (*Haematopus*

*bachmani*), hairy woodpecker (*Picoides villosus*)) that have been observed at the study sites. Each predator species was paired with a non-predator species based on the frequency characteristics of their calls (following Zanette *et al.* 2011). Predator and non-predator species calls paired together were similar in peak frequency ( $t_7 = -1.2$ ,  $p = 0.26$ ), minimum frequency ( $t_7 = -0.3$ ,  $p = 0.80$ ), maximum frequency ( $t_7 = -1.6$ ,  $p = 0.16$ ), and frequency range ( $t_7 = 0.3$ ,  $p = 0.75$ ). Five exemplars of calls from each species were taken from The Cornell Lab of Ornithology and Borror Laboratory of Bioacoustics. The exemplars were randomized to create two 1 h playlists for each treatment. Playbacks were adjusted to broadcast at 80 dB from 1 m away and included a call-to-silence ratio of 1:1.5 following Zanette *et al.* (2011). The interspersed calls and silences simulated temporal variations in predation risk. Furthermore, only one of my three playback units played at any given time and the order in which the units broadcast calls was randomized, ensuring birds did not become habituated to the treatments.

### 2.2.3 Behavioural observations

#### 2.2.3.1 Parental food provisioning

All behavioural observations were conducted solely by me and recorded onto a voice recorder (Sony ICD-PX333) for later transcription. I assessed the response of parents with regard to food provisioning with three measures: feeding visits, feedings per visit and total feedings. A feeding visit was counted whenever a parent arrived at the focal fledgling with food. I was able to confirm that such visits resulted in a feeding either from direct observation or by listening for the distinctive sounds that fledglings make when food is placed in their mouths (Smith 1978). Parent song sparrows are capable of bringing multiple food items in a single visit, so I also counted the number of

feedings per visit, and then calculated the total number of times each fledgling was fed in each 60 min treatment. Total feedings were calculated as the sum of all the feedings at each feeding visits during the 60 min treatment.

I then calculated two values as measures of parental sensitivity to predators based on the counted values of, feeding visits and total feedings, during the two treatments. I calculated these values as the difference in the number of feeding visits and total feedings between the predator and non-predator treatments (predator count - non-predator count). If the difference of these values was negative it would indicate that parents are reducing the amount of food they provided their fledglings during the predator treatment. I would then interpret this reduction in feeding as the sensitivity of the parents to perceived risk or predation, represented by the predator calls. In contrast, I would interpret no change in food provisioning or a positive difference to indicate that parents are not sensitive to the predator calls.

#### 2.2.3.2 Fledgling detectability

Just as with parental behaviours, I described all fledgling behaviours into a Sony digital audio recorder and recorded fledgling vocalizations with a Tascam audio recorder (see Appendix B for observation set up). I assessed the fledglings' response to perceived predation risk by measuring their change in three measures of fledgling visual detectability (concealment, perch height and distance traveled) and auditory detectability (i.e. number of begging vocalizations produced) between the predator and non-predator treatments.

I scored fledgling visual detectability every 10 min, using two variables: 1) height at which the offspring was perched above the ground during the treatments, 2) how concealed a fledgling was. Perch height was scored following Duncan and Bednekoff (2006): **0** = on the ground; **1** = within the 1st m of the ground; **2** = between 1 and 2 m above ground; **3** = between 2 and 3 m above ground etc. Fledgling concealment was scored as either 1 (visible) or 0 (not visible). I then summed the values for each variable to produce an overall score for concealment and perch height per treatment. Lastly, I also measured the straight line distance each fledgling moved within each treatment and approximated the median step distance of the fledgling throughout the treatments. I measured straight line distance covered by the fledglings by marking their position at the start and end position with flagging tape for each treatment and then recording the positions with GPS, in UTM coordinates which I then used to calculate an estimate of the straight-line distance ( $\pm 2$  m error in the GPS) between these two points. I also calculated median step distance during the treatments as a measure of how far fledglings moved. During the treatments, the GPS constantly logged way-points every two minutes, by keeping my distance from the fledgling a constant 8 m, I was able to record an approximation of the fledgling's movements throughout the treatments, and calculate the median step distance at these two minute intervals.

I assessed fledglings' auditory detectability by counting the number of fledgling begging vocalizations in audio files recorded during the manipulations. I was able to record begging vocalizations for 22 of the 44 fledglings I observed. The 22 fledglings that I was not able to analyse begging from, were missed due to a variety of factors. The sound quality of 16 recordings was compromised due to light rain on the speaker (11) and

wind distortion (5). Four of the fledglings begged too softly and did not show up on spectrograms, for confident transcription. The final two files became corrupted and could not be analysed.

Finally, I gauged each fledgling's perception of predation risk by measuring their flight initiation distance (Blumstein 2006; Evens *et al.* 2010, Zanette *et al.* 2011). Animals that are highly sensitive to predation risk typically flee an approaching threat at greater distances than those less sensitive individuals. Starting 8 m away from a fledgling that was engaged in a 'relaxed' behaviour (e.g. preening or perched; following Blumstein 2006), I walked at a constant rate of 0.5 m/s toward the fledgling. When the fledgling moved, I marked my position and measured the horizontal distance (cm) between the researcher and the last location of the fledgling prior to fleeing. Flight initiation distance was only measured once per fledgling, immediately after they had received both playback treatments. This was done so that fledglings and parents were not disturbed during the manipulations.

#### 2.2.3.3 Statistical analyses

I used parental feeding visits, feedings per visit and total number of feedings per 60 min treatment to compare parental provisioning behaviour between non-predator and predator treatments. All three measures were analyzed with repeated measures ANOVAs with treatment (predator vs. non-predator playback) as the repeated measures term. I ran each provisioning measure model with nest number (first or second nest) and treatment order (predator or non-predator playback treatment first) as categorical factors. These

factors showed no main effect or interaction with regard to parental provisioning behaviour, all p-values > 0.30.

As previously mentioned reduced parental provisioning, as a result of fear of predators, has been reported to be associated with reduced nestling survival (Zanette et al. 2011). With this in mind, I wanted to examine whether reduced food provisioning to fledglings was associated in a similar way with fledgling survival from fledge day to the end of the field season, August 31. I accomplished this using a logistic regression model with fledgling fate (alive vs. dead at the end of the field season) as the binary response variable and my approximation parental sensitivity to predation risk, as measured by the change in parental provisioning between the predator and non-predator treatments, as the predictor variable. As fledglings are only cared for by their parents for the first three weeks, examining when the fledglings died was also important. To better understand how when the fledgling died was related to parental sensitivity to perceived risk of predation, I also tested whether parental sensitivity to predation risk was associated with the age at which fledglings died using a Spearman rank correlation with each dead fledgling's age and their parents value of sensitivity to predation risk included.

I next wanted to project what effect reduced parental care due to parents' response to perceived risk of predation would have on fledgling survival at the population level. This would help me to better understand how fledgling survival may be impacted if fear of predators was disrupting parental care throughout the dependent fledgling period, fledge day to independence. Projecting how fledgling survival may be reduced would allow me a more direct comparison to the 40% reduction in the proportion of nestlings that fledged when raised under conditions of high perceived predation risk, previously

reported by Zanette *et al.* (2011). I was able to accomplish this using the logistic regression model previously described to examine whether fledgling fate (alive or dead) was predicted by the sensitivity of their parents to perceived predation risk, based on the difference in provisioning behaviour between predator and non-predator playback treatments. The equation (Equation 1) of this model, describes the relationship between parental sensitivity to perceived risk of predation and the probability of their fledglings being alive or dead, illustrated in figure 4. By taking this equation I could in-put any  $X$ -value or value of parental sensitivity to predation risk, i.e. the difference in provisioning between the predator and non-predator treatments, and it will provide an estimate of the probability of a fledgling surviving under those conditions. In order to project the effect of reduced parental care due to fear on fledgling survival at the population level, I used the population level response of parents, which I calculated as  $X = -3.79$ , the mean reduction in feeding visits parents provided to their offspring when exposed to predator calls. This provided me with an estimate of fledgling survival under conditions where predators are disrupting parental care throughout the post-fledging period. I then compared this to the survival probability estimated if provisioning was not disrupted by predators, under such conditions parents should be feeding their young as much as they can all the time, i.e. feeding visits would remain constant through the entirety of post-fledging period.

**Equation 1: Logistic regression model equation**

$$(1) \quad p = \frac{1}{1 + e^{-(b_0 + b_1 x)}}$$

$x$  = parental sensitivity to perceived predation risk (equation 1).

$b_1$  = coefficient of parental sensitivity to perceived predation risk (equation 1).

$b_0$  = coefficient of intercept.

$p$  = the estimated probability of a fledgling being alive or dead based on the value of  $x$ .

As mentioned in the introduction, offspring mass may predict their survival and mass can be greatly influenced by the quality of parental care the offspring receive (Eggert *et al.* 1998, Krist 2011, Bowen *et al.* 2015). Therefore, I examined the relationship between offspring mass and parental response to perceived risk with a repeated measures ANCOVA. I considered the mass of offspring at the nestling (6 day post-hatch) and fledging (fledge day) stage as repeated measures and the sensitivity of parents to predation risk, difference in provisioning when exposed to predator calls, as the covariate. If the covariate, parental sensitivity to predation risk, showed a significant main effect, it would indicate that sensitivity to predation risk is correlated with offspring mass at both stages. A significant interaction between parental sensitivity to predation risk and offspring mass would indicate that parental sensitivity to predation risk is correlated with one stage disproportionately from the other. While a non-significant result would suggest that parental sensitivity to predation risk has no correlation with the mass

of their offspring. I next tested whether survival was significantly affected by offspring mass using a logistic regression model. Finally, I tested for an interactive effect of parental sensitivity and offspring mass on survival with a Generalized Linear Model with binomial error and a logit link function.

Next I examined how the fledglings themselves may have been modifying their behaviours between the two treatments. I examined how the visual detectability of fledglings varied by testing each visual detectability metric; perch height, concealment, maximum distance moved and median step distance between treatments using repeated measures ANOVAs. Then, I combined my visual detectability measures into one discriminant function analysis (DFA), to determine whether the two treatments could be differentiated this way. As fledgling flight initiation distance (FID) was only measured once per fledgling I tested fledgling response based on the treatment they were last exposed to with a one-way ANOVA.

I also examined if the fledglings modified their begging behaviour between the two treatments as well. Due to the fact that the risk of detection varies not only with how often young birds produce begging vocalizations (Ibanez-Alamo *et al.* 2012) but also with when they produce the vocalizations, with regard to if a parent was present or absent. Begging vocalizations produced in the absence of a parent are potentially more likely to attract predators than when a parent is present (Platzen & Magrath 2004, 2005). With this in mind I separated the begging vocalization based the status of their parent (present or absent) when they were emitted by the fledgling. I then analyzed how the fledglings varied in their auditory detectability with a two-way repeated measures ANOVA, with both playback treatment and status of parent as the dependent variables.

Due to the fact that I observed the sparrows during both first and second nests I ended up with five manipulations where the parents had previously been observed. To ensure that this was not influencing the effect of the treatments I re-fit all of the above ANOVA models as Generalized Linear Mixed Models that included treatment as a repeated measures term and individual nest ID nested as a random effect. The random effect never contributed a significant amount of variation so I present the simpler models, which produced the same results. All data were tested for assumptions of normality and homogeneity of variances using the Shapiro-Wilk W and Levene's tests respectively. I applied BoxCox transformations when necessary and if transformed data still failed the assumptions, they were analyzed with non-parametric tests.

All statistical analyses were run in PASW Statistics 18.0 (IBM SPSS 18.0, Somers, New York, USA) and Statistica 6.0 (StatSoft, Tulsa, Oklahoma, U.S.A). I set alpha at 0.05 and report two-tailed results for all statistical tests. To more easily present the data, all figures and statistical tests report means  $\pm$  1 SE using untransformed data.

## **2.3 Results**

Parental food provisioning to offspring was drastically reduced during the predator treatment. When confronted with the sounds of predators, parents visited their fledglings with food nearly half as often as they did when they heard non-predator sounds (Figure 1; Repeated Measures ANOVA;  $F_{1,42} = 21.62$ ,  $p < 0.001$ ). Parents evidently did not compensate for their lower feeding visits in the predator treatment by feeding their offspring more on each feeding visit. In fact, they fed them less per visit on average, feeding their offspring 27% fewer times per visit during the predator treatment (Repeated

Measures ANOVA;  $F_{1, 42} = 25.62$ ,  $p < 0.001$ ). As a result, it was predictable that the total number of times that parents fed their fledglings during each 60 min treatment was also reduced by nearly half during the predator treatment ( $6.62 \pm 0.81$ ) compared to the non-predator ( $12.11 \pm 0.92$ ; Repeated Measure ANOVA,  $F_{1, 42} = 43.0$ ,  $p < 0.001$ ).

Parental sensitivity to perceived predation risk was a significant predictor of fledgling survival. Fledglings that died were raised by predator-sensitive parents, who reduced their feeding visits on average by 80% during the predator treatment, while offspring that survived were raised by parents less sensitive to the predator treatment, on average only decreasing their food provisioning by only 20% (Figure 2; Logistic Regression, Wald  $\chi = 4.26$ ,  $p = 0.039$ ). Parental sensitivity to predators calculated with the difference in total feedings between predator and non-predator treatments had a similar predictive ability for fledgling fate (Logistic Regression, Wald  $\chi = 5.17$ ,  $p = 0.02$ ). Of the fledglings that died, the majority (77%) died while still dependent on their parents for care (i.e. < 21 day post-fledge). Indeed, I found a significant negative correlation between the sensitivity of parents to perceived risk of predation and the age at which their offspring died (Spearman Rank;  $R = -0.62$ ,  $t_{11} = -2.6$ ,  $p = 0.023$ ), wherein the greater the decrease in feeding visits, when exposed to predator calls, the younger their offspring died.

Based on the population level response of parents to perceived predation risk, measured as the mean reduction in feeding visits, and using the equation of the logistic regression model, I estimated that the probability of fledglings surviving would be  $62.5 \pm 9.17$  % under conditions where predators were disrupting parental care throughout the post-fledging period. In contrast to  $86.0 \pm 9.80$  % estimated survival, if no disruption to

feeding due to fear of predators occurred during the post-fledging period. I then combined this estimated reduction in the probability of fledgling survival, based on my model, with the previously reported 40% reduction in proportion of nestlings fledged from Zanette *et al.* (2011). This combination is best explained by imagining that if at the start of the breeding season there are 100 eggs there would be a 40% reduction in the number that fledged, due to fear effects on parental behaviour. This would leave 60 fledglings, which would be reduced by a further 23.5%, the difference in my two estimates (86% - 62.5%), during the post-fledging period. Based on these calculations, I was able to project that the effect of fear of predators on parental care throughout the brood rearing period, could cause an overall 54% reduction in the number of offspring produced per year.

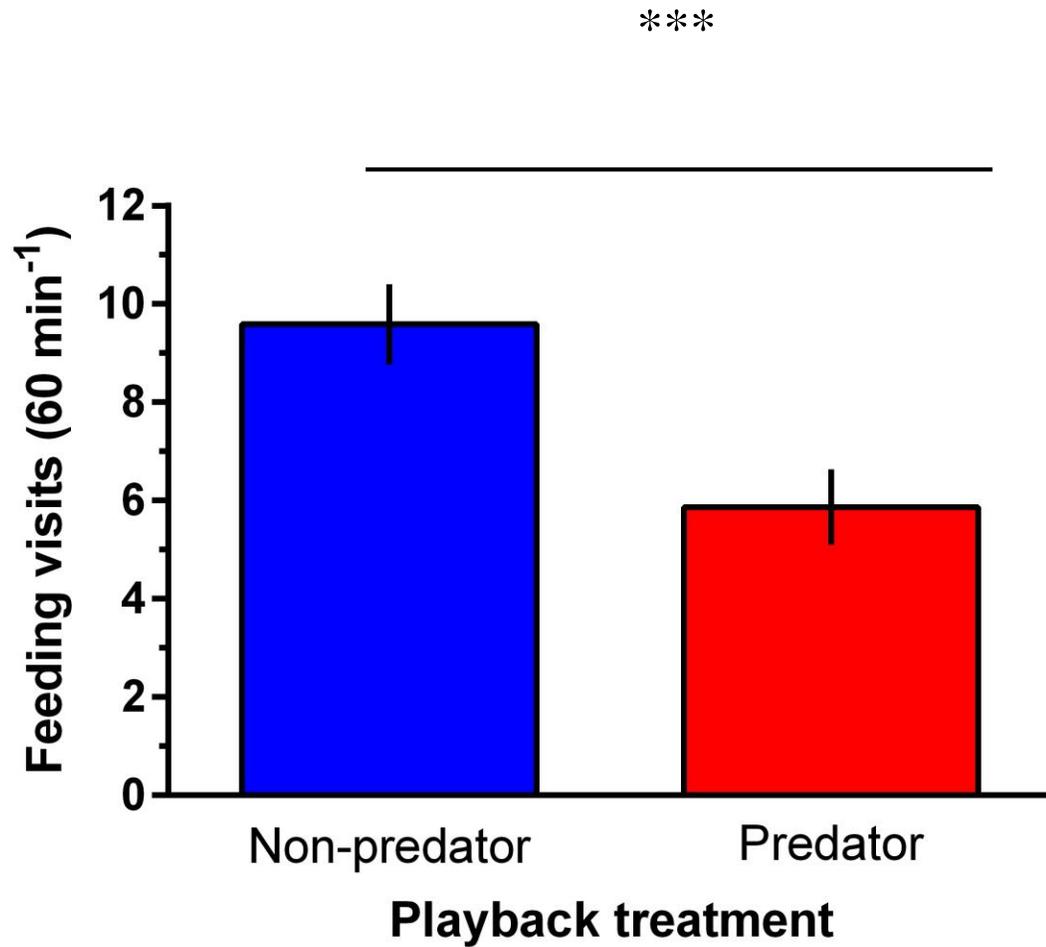
I also found that parental sensitivity to predation risk, as indicated in the change in their provisioning behaviour, was significantly correlated with the mass of their offspring (covariate of parental sensitivity to predation risk: Repeated Measures ANCOVA;  $F_{1,36} = 5.12$ ,  $p = 0.03$ ) at both the nestling and the fledgling stages as indicated by the non-significant interaction (Parental sensitivity to predation risk  $\times$  offspring mass, Repeated Measures ANCOVA;  $F_{1,36} = 0.15$ ,  $p = 0.70$ ). This result indicates that parents who raised lighter offspring were also parents that were most sensitive to increases in perceived risk of predation, who responded to predator sounds by provisioning their fledglings' least. Interestingly, offspring mass was not associated with offspring fate for either nestlings or fledglings,  $20.4 \pm 0.41$  alive vs.  $20.2 \pm 0.30$  g dead fledglings (Generalized Linear Model; Wald = 0.15,  $p = 0.70$ ). Therefore, I tested whether offspring mass might interact with parental sensitivity to predation risk with

regard to fledgling fate and found a significant effect at both the nestling (nestling mass  $\times$  parental sensitivity to predation risk, Generalized Linear Model Wald = 4.74,  $p = 0.03$ ) and fledgling (Figure 3; fledgling mass  $\times$  parental sensitivity to predation risk Generalized Linear Model; Wald = 4.62,  $p = 0.03$ ) stages. As Figure 2 indicates, more predator-sensitive parents ended up with more dead offspring as previously described, and this effect was most pronounced when offspring were heavy but only if they were raised by predator sensitive parents. Thus, heavy offspring typically died if they were reared by parents that responded strongly to predation risk (and dramatically reduced food provisioning when they hear predator calls), but offspring raised by less sensitive parents survived equally well regardless of their mass (Figure 3).

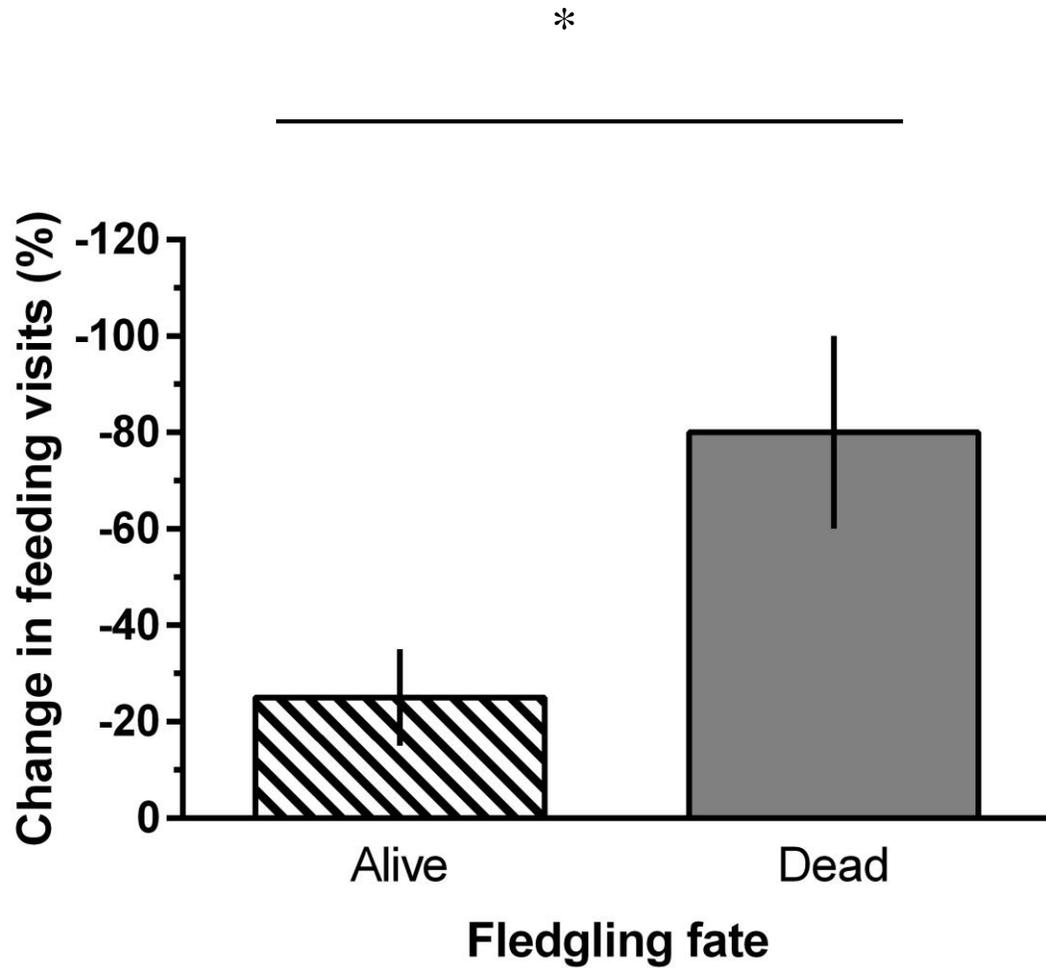
Counter to my expectations, fledglings themselves did not reduce their visual conspicuousness between the predator and non-predator treatments. I found that fledglings received parental food provisioning from similar perch heights ( $1.62 \pm 0.19$  vs.  $1.43 \pm 0.18$ , Repeated Measures ANOVA,  $F_{1,40} = 1.34$ ,  $p = 0.25$ ), were equally concealed ( $1.07 \pm 0.30$  vs.  $1.00 \pm 0.32$ , Repeated Measures ANOVA,  $F_{1,40} = 1.76$ ,  $p = 0.19$ ), had similar maximum distances moved ( $5.83 \pm 1.29$  m vs.  $6.22 \pm 1.27$  m, Repeated Measures ANOVA,  $F_{1,37} = 7.26$ ,  $p = 0.14$ ), and similar median step distance in the predator and non-predator playback treatments, respectively ( $1.15 \pm 0.29$  m vs.  $1.22 \pm 0.27$  m, Repeated Measures ANOVA,  $F_{1,30} = 0.21$ ,  $p = 0.64$ ). Combining all three measures into one discriminant function analysis also did not differentiate between my perceived predation risk treatment groups. Finally, my predation risk treatments did not lead to significant differences in the distance at which fledglings fled an approaching threat

(Flight Initiation Distance;  $113.5 \text{ cm} \pm 19.42$  vs.  $150.5 \text{ cm} \pm 22.42$ , predator vs. non-predator respectively; 1-way ANOVA,  $F_{1, 19} = 1.55$ ,  $p = 0.23$ ).

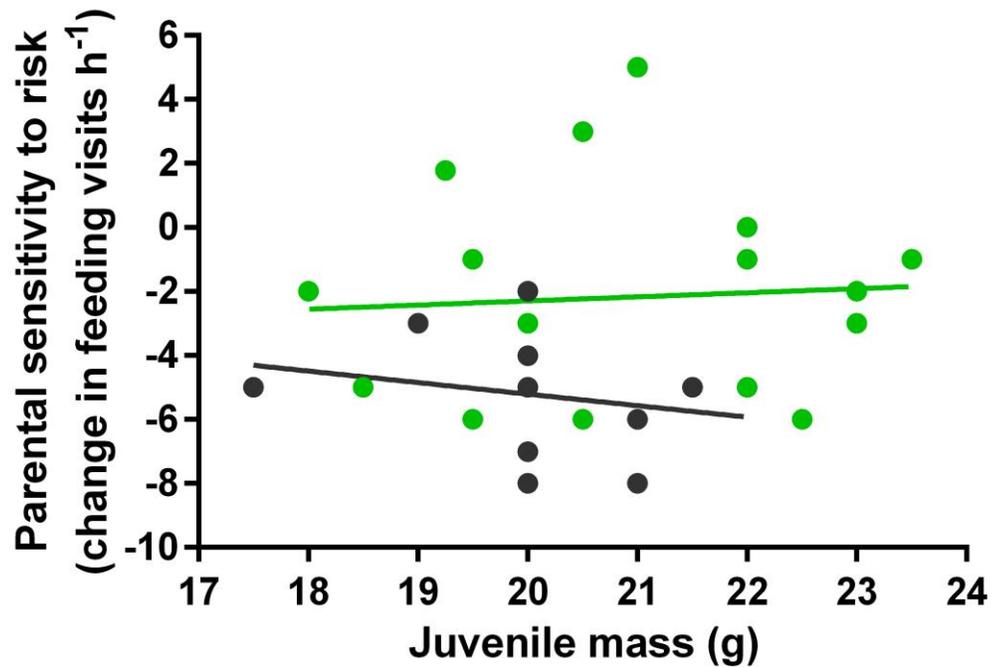
Similarly, fledglings did not respond to the predator treatment by reducing their begging vocalizations, emitting a similar number of vocalizations between non-predator and predator treatments ( $105.2 \pm 28.09$  vs.  $117.03 \pm 35.53$ , Two-way Repeated Measures ANOVA;  $F_{1, 16} = 0.33$ ,  $p = 0.57$ ). This is surprising as young birds tend to produce many more vocalizations when they are fed, and when combined with the fact that during the treatments fledglings were fed so much more, in the non-predator than the predator treatment, I would expect that begging vocalizations would be higher there. However, this was clearly not the case. This is explained by the significant interaction between parental status (parent present or absent when vocalization was emitted) and treatment (predator vs. non-predator). Fledglings produced more vocalizations during the predator treatment than the non-predator treatment, when no parent was present (Figure 5; playback treatment  $\times$  parental status,  $F_{1, 16} = 10.58$ ,  $p = 0.005$ ). In contrast, fledglings produced a similar number of begging vocalizations during both treatments when a parent was present.



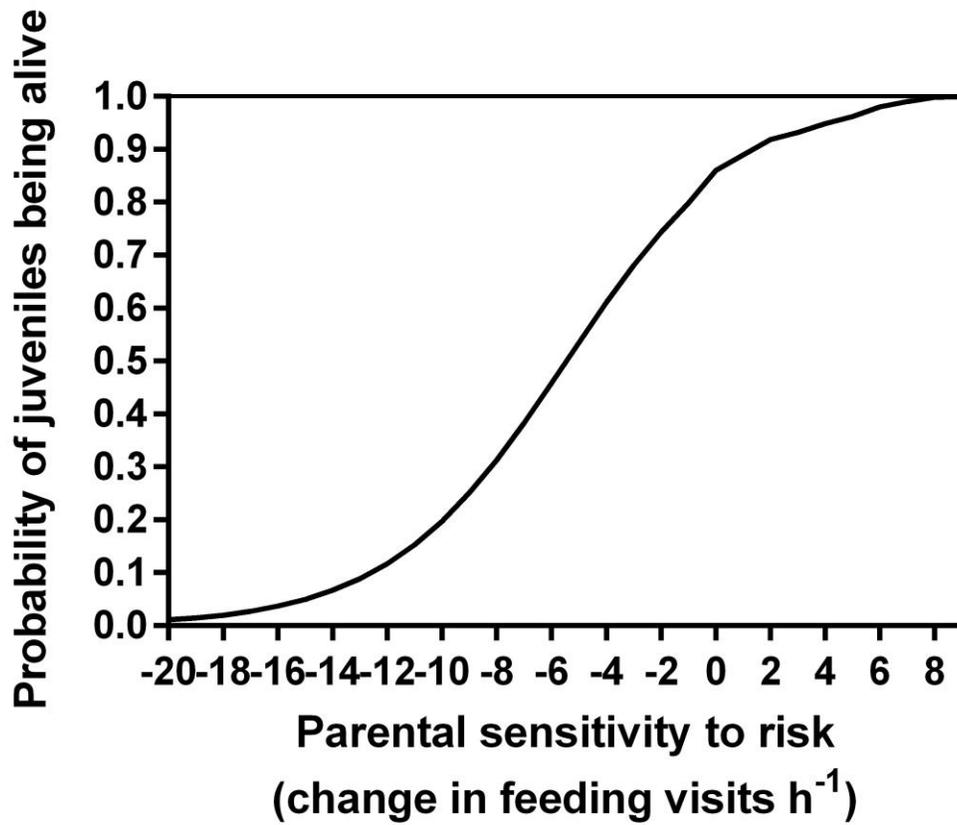
**Figure 1.** Comparison of feeding visits parent birds made to their offspring during the low perceived risk non-predator treatment (Blue) and high perceived risk predator treatment (Red). All values are mean  $\pm$  1 SE.



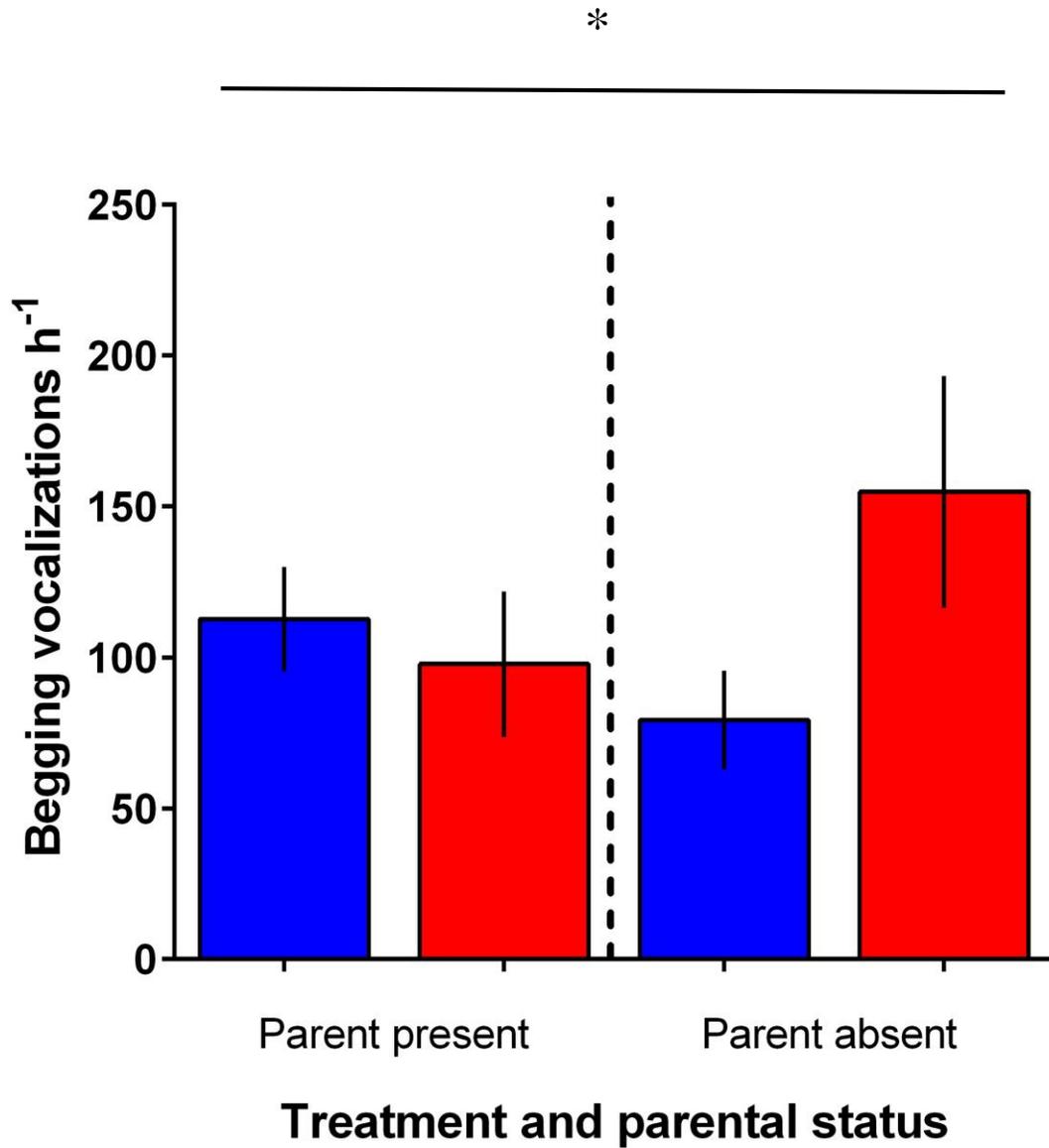
**Figure 2.** Comparison of percent reduction in feeding visits (visits during the predator treatment minus visits during the non-predator treatment) parent birds made to offspring survived (Barred fill) and those that died (Grey fill) during the course of the study. All values are mean  $\pm$  1 SE.



**Figure 3.** Interaction between juvenile mass and parental sensitivity to predation risk (feeding visits during the predator treatment minus feeding visits during the non-predator treatment) with regard to fledglings' fate at the end of the experiment represented by the lines of alive (Green) and died (Grey) juveniles.



**Figure 4.** The plotted probability of a juvenile being alive estimated by the equation of the logistic regression model which describes the relationship between juvenile fate and the sensitivity of their parents to predation risk based on the data I collected.



**Figure 5.** Comparison of fledgling begging vocalizations during the non-predator treatment (Blue) and predator treatment (Red), during periods when the offsprings' parents present (coming towards the fledgling with food or feeding it) and when they were absent. All values are mean  $\pm$  1 SE.

## 2.4 Discussion

My manipulation demonstrates that the fear of predators has a dramatic effect on parental care provided to fledged offspring and that this in turn is a major factor determining whether offspring live or die. Under experimentally manipulated perceived predation risk, parents drastically decrease their feeding visits to fledglings. Parents also reduced the number of feedings they provided at each visit. The combination of decreased provisioning visits and feedings at those visits resulted in the decrease in total number of feedings that offspring received over the course of the predator treatment. These three measures confirm that the responses displayed by the parents, in response to perceived risk, were in fact restricting the nutrition their offspring received. Consequently, fledglings with parents that were most sensitive to perceived predation risk were more likely to die. Moreover, my results from the logistic regression model estimates a 24% decrease in the number of surviving fledglings based on the average parental response to perceived predation risk and that when combined with the 40% reduction in proportion of nestlings that fledged (Zanette *et al.* 2011) perceived risk is projected to cause an overall 54% decrease in offspring survival. More predator-sensitive parents also rear lighter offspring, but offspring mass alone was not predictive of offspring survival. Despite this, the interaction between offspring mass and parental sensitivity to predation risk with regard to juvenile survival suggests that heavy fledglings with sensitive parents were at an increased risk of dying, while fledglings survived equally with less sensitive parents regardless of their mass. Counter to predictions, fledgling song sparrows actually appeared to increase their acoustic detectability during the predator treatment. In fact, fledglings produced more begging vocalizations during

what should be perceived as a high risk time i.e. during the predator treatment and while no parent was near them. I suggest that this result reflects the fact that fledglings' need for food rather than their perception of predation risk is driving their begging behaviour.

This study demonstrated that perceived predation risk had a dramatic negative affect on the quality of parental care parent birds provided to their offspring during the post-fledging period. Parental care is a critical factor both in length and quality for the survival of many animals (Grueebler & Naef-Daenzer 2010; Maniscalco 2014). Despite the importance of the post-fledging period, it has not been well examined in birds, with only a handful of studies that have actively recorded parental care beyond the in-nest period (reviewed by Cox *et al.* 2014; Gow & Wiebe 2014). In fact, other than reporting that the post-fledging period is a time of high mortality, past research is very limited with regard to what is happening to birds after they leave the nest (reviewed by Cox *et al.* 2014). I know of only four publications which directly measured known fate of fledglings and included parental care as a factor, three of which found parental care to be a significant covariate with offspring survival (Wolf *et al.* 1988; Adams *et al.* 2001; Naef-deanzer *et al.* 2008, 2010). I was able to not only directly follow fledgling survival, but my research is unique in that I was able to predict offspring survival by specifically focusing on parental response to perceived risk. Reduced feeding visits during the predator treatment signify that perceived risk of predation compromises parental care, and further, that the sensitivity of parents to this risk is related to their quality as parents. Not only did parents decrease how much they fed their fledged offspring, but this reduction was almost identical in magnitude to that observed in parents during the in-nest period, during manipulations of perceived predation risk (Zanette *et al.* 2011). This

suggests that the increased nutritional needs of older offspring do not influence the response of parents under perceived risk of predation. While I did not measure the size of food items, my findings that feedings per visit also significantly decreased suggests that no compensation for decreased feeding visits was made by parents. As young animals grow their demand for food increases and this in turn should facilitate increased feeding visits by parents (Smith *et al.* 1978; Gruebler & Naef-Daenzer 2010; Tarwater & Brawn 2010; Naef-Daenzer *et al.* 2011). By not compensating for this reduction in feeding, I can ascertain that this response by parents to increased risk is straining the nutritional demands of their young. This suggests that even as demand for nutrition increases with offspring growth, the parents' behavior is still driven by the risk posed by the predators. This effect on parental care does, in fact, have an effect on offspring survival, as indicated by my results, that parental sensitivity is predictive of juvenile fate. While, previous publications examining the effect of perceived risk of predation on parental care (Peluc *et al.* 2008; Eggers *et al.* 2008; Kozlovsky *et al.* 2015) and those that look at consequence to demography (Karels *et al.* 2000; Zquette *et al.* 2011) have been limited to this in nest phase, my results demonstrate that these previous studies do not encompass the full effect fear of predators has on parental care nor the subsequent consequences for population growth.

One of the most impressive aspects of my findings is the striking ability of my short-term assay to describe so much about the organisms I directed it at. Using only a simple comparison of parental provisioning behaviour between two playback treatments I was able to produce a metric which was not only predictive of offspring survival but also reflected the offspring's physical condition both as nestlings and as fledglings. The

difference between the number of feeding visits in the non-predator and predator treatments, allowed me to predict if offspring would be alive or dead at the end of the study. Additionally, I found that this parental sensitivity to perceived risk was correlated with the age at which these same offspring expired, with offspring dying at younger ages with increased sensitivity. I then took this same measurement of parental sensitivity and was able to categorize the mass of offspring, as both nestlings and fledglings, based on their parents' response, with parents that decreased feedings having young of lower masses. These results demonstrate the implications this simple assay has in regard to the study of the behaviour and demography of wild populations of birds. By simply observing parental behaviour during the treatments, a researcher is presented with a battery of knowledge regarding the life history of their subjects, which would otherwise likely require several individual measurements.

The negative correlation I report, between parental sensitivity to predation risk and the age at which offspring died, indicates that not only does reduced provisioning in response to predation risk predict reduced survival but that the sensitivity of parents leads to their young dying at younger ages. Further, the majority of fledgling mortality that I observed occurred in the first four weeks post-fledging when the birds are still dependent on their parents. This suggests that it is the effects on parental care that are driving fledgling survival as opposed to additional factors. The pattern of fledgling mortality I found is in keeping with what is reported in the literature regarding passerine birds (Rush & Stutchbury 2008; Grueebler & Naef-Daenzer 2010; Dybala *et al.* 2013; Gow & Wiebe 2014; Allen *et al.* in preparation). This high mortality during the first four weeks post-fledge has previously been attributed to the fledglings' inability to feed themselves or to

correctly assess threats from predators (Grueebler & Naef-Daenzer 2010). Quality of parental care is of critical importance to the survival of young animals, with individuals that receive higher quality care having a greater likelihood of survival (Gueebler & Naef-Daenzer 2010; Lehtinen *et al.* 2014; Maniscalco 2014). My findings further highlight the significance of parental care and the influence that fear of predators has on the survival of dependent offspring.

The effect of perceived risk or predation on parental care was not limited to my treatment period. This was highlighted by the results of my logistic regression results regarding the predictive properties that parental response to predation risk had with regard to offspring survival. The fact that highly sensitive parents, those that attenuated feeding visits, had lighter offspring throughout the brood rearing stage, both as nestlings and fledglings, lends further support to this concept. My analysis of offspring mass indicates that parents who were sensitive to risk during the treatment periods reared offspring of lighter mass throughout the brood rearing period, both pre- and post-fledge, suggesting that the reduction in parental care they exhibit is persistent and representative of their overall poor parental care. This is supported by Zanette *et al.* (2011) who demonstrated that parent song birds raised lighter nestlings due to reduced parental care following exposure to experimentally increased perceived risk during the entirety of in-nest stage. I conclude that even small fledglings, which should have a reduced need for food (Moreno *et al.* 1997), are not able to persist when their parents responded strongly to perceived risk of predation, and fledglings of high mass, which should require even more food, appear to fair the worst when cared for by sensitive parents. In contrast,

parents that were insensitive to the predator manipulation had longer surviving young regardless of their mass.

My results demonstrate the drastic negative effect that perceived risk of predation has on parental care during the post-fledging period. This reduction in parental care not only has severe consequences for offspring survival but significant population level effects. Based on logistic regression model and the mean response to risk of predation, I predict that parent song sparrows' response to predators decreases their offspring's probability of survival by 24% in addition to the previously reported 22% reduction to nestling survival found by Zannette *et al.* (2011). These findings further demonstrate that the total impact of perceived risk of predation has on song sparrow demography is likely greater than that due to direct killing (Creel *et al.* 2007; Creel & Christianson 2008; Sheriff *et al.* 2009), and that this effect is even more detrimental to population growth than what has been demonstrated until now (Zannette *et al.* 2011). These findings are consistent with the hypothesis proposed by Zannette *et al.* (2011) that fear of predators would continue to compromise parental care to fledglings leading to a decrease in population growth even greater than that found during the in-nest stage alone. Previous studies (Creel & Christianson 2008; Zannette *et al.* 2011) examining the effect of perceived risk of predation on free-living prey demography have demonstrated impressive effects on reproductive success (i.e. ~40% reductions in both pregnancy in elk and in the number of offspring fledged in song sparrows). However, these studies on offspring production have been limited either by examining only a portion of the reproductive period, during pregnancy or while in the nest (Creel *et al.* 2011; Zannette *et al.* 2011) or by being conducted without the ability to separate the effects of direct

removal by predators from those of perceived risk of predation (Christianson & Creel 2014). The results I report not only document the effects of predation risk during a previously unexplored time in offspring survival, the post-fledging period, but also integrate these novel findings with prior knowledge, about the in-nest period, to produce a complete prediction of the drastic negative impact, 33% decrease, perceived risk alone can have on prey survival. The effect of perceived predation risk on population growth rate is most likely even greater still than the 33% reduction in offspring survival documented here resulting from the effect on parental care. Song sparrows laid and hatched fewer eggs due to perceived predation risk (Zanette *et al.* 2011). While, Allen *et al.* (in preparation) suggests that offspring raised, in an environment with high perceived risk of predation suffer greater mortality rates due to mechanisms, independent of those that I documented, such as long term effects on behaviour and physiology.

In contrast to the drastic response that parents exhibit during the predator treatments, fledglings did not reduce their visual detectability and actually appear to have increased their auditory detectability, suggesting that fledglings are in fact incapable of interpreting predator calls as an indication of risk. The behaviour of the fledglings themselves could influence how detectable they are and lead predators to their location (Ritchison 1997; Anders *et al.* 1997; Balogh *et al.* 2011). I found that fledglings produced more vocalizations during what should be the most dangerous time, while the predator treatment was on without their parents present. This response from fledglings suggests that they do not recognize the predator cues that I presented to them. This is surprising considering the finds of Magrath *et al.* (2007) and Haff & Magrath (2010) who experimentally demonstrated that nestling white-browed scrubwrens (*Sericornis*

*frontalis*) became silent, stopped begging, when exposed to the sounds of a major predator walking on dry leaves. This contrast in responses is likely attributed to a difference in the type of stimuli, predator calls vs. sounds of movement, the young in each study were exposed to. Sounds of movement next to the nest represent an immediate threat to survival that is not necessarily conveyed by the calls of a predator. I know from personal experience that fledglings in my system are not completely naïve to potential threats. This is evident during fledge day captures with fledglings fleeing my approach and remaining silent for long periods after failed attempts. These stimuli are similar to those used by Magrath *et al.* (2007) and therefore it is conceivable that nestlings in their system would be equally unresponsive to predator calls themselves. With the risks so evidently incurred by begging, my results indicate that fledglings are either oblivious to or outright ignoring the danger posed by the predators in their environment and are only responding to their hunger which is a product of the reduction in parental care in response to perceived risk. This lack of response to predator calls is likely a factor in the high mortality seen in young particularly in the first few weeks after fledging as they learn to recognize predators. These findings support those reported by Grueebler & Naef-Daenzer (2010), who suggest that fledgling survival was negatively affected when parents cut parental care short, which Grueebler & Naef-Daenzer (2010) attributed to the offspring's poorly developed skills in detecting predation threats. Increased begging to attract parental care likely explains why I see no significant change in the number of vocalizations produced by fledglings between treatments. With fledglings increasing their vocalizations during the predator calls, when feeding visits are reduced, balancing out the number of calls during the non-predator calls when parents are visiting frequently and

thereby stimulating fledgling begging (Ritchison 1997). This also indicates that begging in fledglings was an indication of need for nutrition just as it was with nestlings. Begging vocalizations increased as parents decreased their provisioning rates during the predator treatments (Budden & Wright 2001; Rastogi *et al.* 2006; Krauss & Yasukawa 2013).

Though my results conclusively demonstrate that parent sparrows respond to perceived risk of predation beyond the in-nest stage and into the post-fledging stage, I cannot definitively say whether the response of parents' was the result of parents avoiding predators themselves or their attempt to prevent detection of their young. The parents themselves may increase the detectability of their young through repeated visits, drawing the attention of predators to their location (Skutch 1949). Therefore, it is reasonable to interpret the response by parents as an effort to reduce the likelihood of their young being detected. Past studies examining the effect of predation risk on parental care, during the nestling stage, suggest that parents decrease feeding visits to reduce the detectability of their offspring to predators (Peluc *et al.* 2008; Ghalambor *et al.* 2013). This likely explains at least part of this response in my system, with fledglings being particularly conspicuous as a result of intense begging at their parents' feeding visits (McDonald *et al.* 2009; Ibanez-Alamo *et al.* 2012). The fact that I found that parents brought their offspring fewer feedings per visit suggests that the perceived risk of predation is negatively affecting the foraging ability of the parents themselves. It is therefore probable that the risk of predation is greatest for the parents and they are engaging in anti-predator behaviours which keep them from foraging and feeding their offspring. This hypothesis is further supported by the lack of response seen from the offspring themselves.

My results demonstrate that non-consumptive effects of predators have negative consequences for dependent post-fledged offspring through reduced parental care. I was able to predict that fledgling survival was reduced by 24% due to effects on parental care and that when combined with past findings regarding the in-nest stage that perceived risk of predation resulted in an overall 54% reduction in offspring produced per year. These findings support previous hypotheses that the fear of predators has an even greater effect on population growth than what has been previously reported. I found that parents nearly halved their provisioning to their offspring under conditions with perceived risk or predation. Furthermore, how sensitive these parents were to risk cues was indicative of the mass and predictive of survival of their offspring. Parents that decreased feedings to a greater extent had lighter offspring that were more likely to die. Survival of fledglings may further be reduced through their increased detectability by predators, as a result of a greater number of begging vocalizations produced in an effort to compensate for reduced parental care. I suggest that the effects of fear of predators on prey population growth are not limited to that which has been reported with regard to fewer offspring produced during the in-nest period. Future studies should focus on filling the gap of how perceived risk of predation affects recruitment from year to year and lifetime reproductive success.

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## Chapter 3

### General Discussion

The objective of my thesis was to further examine the effects that the perceived risk of predation can have on prey species in order to fill an integral missing link in this already well-studied and ever expanding component of biological research. In Chapter 1, I compiled a review of how predation risk can have all-encompassing effects on prey that range from the population to the individual level. I provided a specific focus on the effect of perceived risk of predation on prey demography and highlighted areas that lacked examination in avian species.

In Chapter 2, I explored the responses of family units of song sparrows (*Melospiza melodia*) to perceived risk of predation. I exposed parent sparrows and their offspring to short term increases in the level of perceived risk through the use of audio playbacks and measured the change in food provisioning parents provided to their young as well as the offsprings' responses during the post-fledge period. I then tracked the fate of these same offspring and used the measurements on parental care to explain the trends in survival.

I then integrated these findings on parental care and offspring survival during the post-fledgling period with prior findings to build a comprehensive examination of predator effects on parental care and offspring survival. In this final chapter, I aim to summarize the broader biological significance of my findings and discuss the impact of predation risk on conservation management. I will also outline some of the challenges facing study of behaviour during the post-fledgling period and provide some future

directions to further explore when researching perceived predation risk effects on demography.

### **3.1 Predators affect prey populations**

I tested whether and to what extent perceived risk of predation influences parental care and offspring survival in wild populations of a terrestrial vertebrate prey species. In my field experiment, parents under increased perceived risk of predation reduced feedings to their offspring by nearly 50%. This response of parents was predictive of their offspring's survival (i.e. as feedings decrease the likelihood of survival decrease as well). Overall, my results suggests that perceived risk of predation reduces survival of offspring by 24% during the post-fledging period; in addition to the 23% reduction risk that has been demonstrated to occur while the young are in the nest as reported by Zанette *et al.* (2011).

My results, along experimental evidence from other systems, suggest that risk of predation alone is likely to affect the majority of prey species at the population level, regardless of the taxonomic affiliation or the trophic position of the prey species (Creel & Christianson 2008; Zанette *et al.* 2011; Christianson & Creel 2014). Further, these results demonstrate that this effect of predation risk is not limited to the parts of animal life-history that have previously been examined.

My results indicate that not only do predators affect at least one determinant of change in population size, net offspring production, but that the magnitude of this effect is even more staggering then previously measured. My short term assay was capable of not only predicting the survival on individual song sparrow fledglings but also had the

capacity to explore the effect perceived risk of predation has on population growth its self.

My results also demonstrate that the parents' response to threat may also have effects on the quality of the offspring produced. This suggests the risk of predation may also have intergenerational effects, so that the risk of predation on a single generation of prey may be transmitted to later generations as well. My findings further support the fact that that the risk of predation should be incorporated into both conservation and management planning and current ecological theory, and that this factor has to be incorporated into all stages of the parental care period.

### **3.2 Consequences for applied conservation**

In ecological systems, which are diverse and dynamic in nature, recent research has demonstrated that perceived predation risk constitutes a significant factor in the shaping of prey demography as well as ecosystem function (Creel & Christianson 2008; Estes *et al.* 2011; Zanette *et al.* 2011; Christianson & Creel 2014; MacLeod *et al.* 2014). While there is little doubt that predators, particularly introduced predator species, often contribute to the decline of prey populations (Salo *et al.* 2007), it is clear that predators affect prey populations to a far greater extent than by just removing individuals, as indicated by the vast body of research on non-consumptive effects, my own findings included (Preisser *et al.* 2005; Wirsing & Ripple 2011; Zanette *et al.* 2014). Despite this, many management plans, seeking to increase populations, only implement protocols to protect prey from direct predation, ignoring the effects that perceived risk of predation have completely (Isaksson *et al.* 2007).

Neglecting to account for the contribution of non-consumptive predator effects often results in a massive underestimate of the total effect of predators on these sensitive prey populations (Peckarsky *et al.* 1993). Luttbeg & Kerby (2005) estimated that approximately half of the total effects of predators are overlooked when non-consumptive predator effects are disregarded, which suggests that merely protecting prey (i.e. predator exclusion) from direct killing may not diminish predator effects sufficiently to allow these prey populations to recover. Additionally, many of the implications used can only protect prey while they are in the nest (Peckarsky *et al.* 1993); however high predation rates still occur when young first leave the nest (Cox *et al.* 2014). My results demonstrate that the perceived risk of predation still strongly influences the survival after departure from the nest. The complete removal of predators may prove to be more effective in conserving declining prey populations than only preventing direct killing, as removing predators eliminates both consumptive and non-consumptive effects. Moreover, as food and predators have synergistic effects on prey populations (Zanette *et al.* 2003), implementing a supplemental food program for threatened prey species in tandem with reducing predator numbers may aid in conservation. This is due to prey animals' improved capability to access and assimilate food, and limited energy expenditure on predator avoidance behaviours, when the perceived risk of predation is low (Hawlana & Schmitz 2010).

Measuring the population level effects of perceived predation risk is an overwhelming task that involves analyzing several components which can influence prey demography (Liley & Creel 2008; MacLeod *et al.* 2014). As mortality can result from factors related to anti-predator behaviour (i.e. starvation) and at multiple stages (i.e.

nestling, fledgling, juvenile etc.), it is critical to examine predator effects at all stages of a prey species in order to predict predation risk effects at a population level (Zanette *et al.* 2011). However, this is not a simple task particularly with regard to most vertebrate species. This is largely due to the high mobility of these animals, making it difficult to measure known fate and therefore to understand what is happening in that particular population. The results of my experiment, while not directly measuring the total effect of perceived predation risk on survival, allow me to predict the total influence of non-consumptive predator effects on offspring while in the care of their parents. My findings conclusively reported the effect fear of predators has on prey preproduction at a stage that had never previously been examined. These findings help clarify just how all-encompassing the effects of perceived risk are on prey populations, and should further illustrate to conservation programs just how necessary it is to incorporate these factors into their operations.

### **3.3 Challenges facing research on population level effects of fear in vertebrates**

As previously mentioned, in order to obtain a full understanding of demography and particularly the effects of perceived risk of predation on prey populations, it is necessary to have a detailed knowledge of the number of offspring produced by a female in a given year, as well as rate of mortality for the population (Krebs 1999). This is relatively simple for researchers working on invertebrates and aquatic species, who can either replicate natural conditions (i.e. microcosms) in the lab or have study subjects confined to water bodies (Schmitz *et al.* 1997; reviewed in Preisser *et al.* 2005). In contrast, things are not so simple when it comes to examining terrestrial vertebrates

(Zanette *et al.* 2011), which in general have a much greater potential for mobility and dispersal as well as requiring much larger areas for natural behaviour.

In birds specifically, population biology is incredibly biased and mostly limited to the in-nest period, counting eggs produced and offspring that leave the nest. However this is where the majority of studies end with regard to direct measurement, with many relying on re-sighting or re-capture date for survival beyond this point (reviewed by Cox *et al.* 2014). The increasing availability and use of lightweight radio transmitters has, to some extent, expanded the ability of researchers to accurately measure known fate beyond the nest. Despite this improvement in technology, studies are still extremely limited in number (Cox *et al.* 2014). This limitation in accurate survival data makes it likely that the majority of programs focused on species at risk are dealing with population models that may be extremely unrepresentative and likely underestimate mortality beyond the nest (reviewed by Cox *et al.* 2014). Regardless, more studies that follow individuals over the entirety of a year are needed to provide accurate population data. The survival data I present in chapter 2 helps to add to this extremely limited facet.

In an ecological context where predators so clearly have wide ranging effects on prey populations, it is critical to our understanding to include these effects when examining total population level effects (Zanette *et al.* 2011). Measuring direct predation effects, where predators kill and eat prey is relatively simple with the examination of predator diet or the collection of corpses particularly when this is paired with radio tracking studies (Salo *et al.* 2007). However, the process is not so simple for non-consumptive effects on survival, particularly when the underlying causes of fate are

cryptic, such as poor physical condition due to elevated perceived risk leading to starvation or easy capture by predators as suggested by Zanette *et al.* (2011).

Using audio playbacks is an invaluable tool when examining predation risk effects, as they allow investigators to artificially manipulate the risk prey perceived of being killed in their environment without actually manipulating live predators. This also offers a controlled and highly repeatable level of risk lending its self readily to robust research (Blumstein 2006). My findings are an excellent demonstration of this, by using only a simple comparison of parental provisioning behaviour between two playback treatments I was able to produce a metric which was not only predictive of offspring survival but also reflected the offspring's physical condition over time. Of course, this type of measurement is only possible when paired with a radio tracking study for known fate of individual. The power that this simple assay has demonstrates the value this type of manipulation can have to the ecological community.

My findings help to fill the final gap, the post-fledging period, in our understanding of how perceived predation risk effects parental care and offspring survival. However, in order to have a complete understanding of the population level effects of predation risk extensive research still needs to be conducted with regard to what occurs after the breeding season.

As with many vertebrates, once offspring become independent of their parents they disperse, emigrating to nearby territories, and in many species both adults and juveniles have an annual migration (Dybala *et al.* 2013). This makes it difficult for classical radio tracking to follow survival of tagged individuals as they can quickly move

out of range or simply cover too much distance for this type of technology to logistically be effective. There is potential for the use of satellite tags to provide more long-term data on survival and allow for a more complete understanding of the long-term effects of predation risk. However, these tags are still generally too expensive to allow for large sample sizes at this point in time. Focusing on species and populations that are non-migratory, such as the song sparrows in the Gulf Islands, may be the best strategy in the short term for developing a better understanding of risk effects endured both during development and during the rest of an individual's life, though even these populations have a high level of emigration (Zanette et al. 2006).

### **3.4 Future directions**

The next major step in the examination of the effects of perceived predation risk on prey demography should be to explore its influence on overwintering survival of both juvenile and adult birds as well as other vertebrate taxa. This examination is likely best through a combination of large scale manipulation similar to that conducted by Zanette *et al.* (2011) during the breeding season, short term treatments such as the one I describe in chapter 2 and long term radio or satellite tracking of individuals. In these experiments, the environmental level of perceived risk of predation can be manipulated, and paired with tracking the survival of both fledglings and parents tracked until recruitment the following spring. The examination of this final stage of avian life history would provide ecologists, as a whole, with a comprehensive illustration of predator effects on behavior and survival even if it were in a relatively simple system (i.e. non-migratory).

The recent surge in research on non-consumptive predator effects has clearly demonstrated that they are pervasive in ecological systems. Several experiments have established that the effects of perceived risk of predation on prey at the individual level transfers up to the population level, and suggest that this in turn can alter entire ecological communities as well (Preisser *et al.* 2005; Zanette *et al.* 2011; Christianson & Creel. 2015; Suraci *et al.* in preparation). Preisser *et al.* (2009) suggested that high variability in environmental conditions (e.g. climate or resource variability) may aggravate the costs of perceived predation risk for prey. My study controlled for environmental stochasticity by running during a single year, in relatively homogeneous habitats. However, as climate change is projected to significantly alter ecosystems, future research must include multi-year experiments to evaluate the role environmental conditions play in these effects (Peckarsky *et al.* 2008). Experimental tests of the predictions from theory may provide insight into possible interactive effects of biotic factors in modifying indirect predator effects.

In addition, there is a growing body of research that demonstrate the cascading effects that predators can have on ecosystems (reviewed by Estes *et al.* 2011). Manipulations conducted on invertebrate and aquatic species in experimental mesocosms have demonstrated not only that predation risk can affect the fecundity and survival of prey, but also that these effects can have cascading consequences down food chains (i.e. influencing soil composition etc.; Preisser *et al.* 2005). Large vertebrate predators are known to alter plant communities through the removal or control of primary herbivores, potentially improving habitat for other species, with song birds being likely beneficiaries (McLaren & Peterson 1994; Ripple & Beschta 2003). This is likely not the limit of

predator cascades in ecosystems, recent work by Suraci *et al.* (in preparation) has demonstrated that risk of predation can have significant effects on organisms over multiple trophic levels. These findings provide an interesting line of questioning for future investigators particularly those interested in conservation, where native and non-native mesopredators are the primary predators.

Future research should no doubt focus on how these trophic cascades could be implemented in the conservation of species. This could be accomplished through examination of the effect of manipulating the perceived risk these mesopredators experience and the subsequent changes that occur to the populations of their prey. The gulf island ecosystem system is an ideal for this type of investigation. Raccoons (*Procyon lotor*), the major mesopredator, have already been described to have drastic impacts on a wide spectrum of prey populations in this system (Suraci *et al.* 2014). The interaction between raccoons and song sparrows (*Melospiza melodia*) would make an exemplary model system to test the effect of artificially increased predation risk to raccoons on the survival of sparrows. Such research could have major implications for programs looking for alternative methods of controlling predators of their focus species.

Over all, the results from my study and other experiments on non-consumptive predator effects announce a paradigm shift in the approaches population and community ecologists need to take in investigating populations and ecosystems. Future research will likely only provide further support for Creel and Christianson's (2008) contention that non-consumptive predator effects ought to be more fully incorporated into general ecological theory.

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## Appendices

**Appendix A.** Picture of one of the portable playback units.



**Appendix B.** Picture of the behavioural observation set up



**Appendix C.** Picture of two-day old fledgling equipped with radio



**Appendix D.** Ethics approval for animal use

AUP Number: 2010-024

**PI Name:** Zanette, Liana

**AUP Title:** The Effects Of Predators And Predator Risk On Prey: From Genes To Ecosystems

**Approval Date:** 04/04/2014

**Official Notice of Animal Use Subcommittee (AUS) Approval:** Your new Animal Use Protocol (AUP) entitled "The Effects Of Predators And Predator Risk On Prey: From Genes To Ecosystems" has been APPROVED by the Animal Use Subcommittee of the University Council on Animal Care. This approval, although valid for four years, and is subject to annual Protocol Renewal. 2010-0245

This AUP number must be indicated when ordering animals for this project. Animals for other projects may not be ordered under this AUP number. Purchases of animals other than through this system must be cleared through the ACVS office. Health certificates will be required.

The holder of this Animal Use Protocol is responsible to ensure that all associated safety components (biosafety, radiation safety, general laboratory safety) comply with institutional safety standards and have received all necessary approvals. Please consult directly with your institutional safety officers.

Submitted by: Copeman, Laura on behalf of the Animal Use Subcommittee University Council on Animal Care

## Appendix E. Playback information

### 60 min playback playlists

I obtained all of the playback calls from the Macauly Library Database (Cornell University Lab of Ornithology, Ithaca, New York, USA). All sounds were edited in Audacity (Audacity 2.1.0 ®; Mazzoni 2015) and RavenLite (Version 1.0, Cornell University Lab of Ornithology: Bioacoustics Research Program, 2010) to eliminate noise, shorten calls to the proper length and to amplify the files to broadcast at 80 dB at 1 m (following methods of Peluc *et al.* 2008 and Gahlambor *et al.* 2013). I used four predator species known to prey upon song sparrows and which occur in the southern gulf islands of British Columbia; (common raven (*Corvus corax*); Cooper's hawk (*Accipiter cooperii*); Merlin (*Falco columbarius*); sharp-shinned hawk (*Accipiter striatus*)) and four non-predator species Canada goose (*Branta canadensis*); northern flicker (*Colaptes auratus*); black oystercatcher (*Haematopus bachmani*); hairy woodpecker (*Picoides villosus*)). I used 5 different exemplars representing 5 different individuals of each species, each individual file 20 in total was paired with a corresponding control call based on a qualitative assessment of their sounds in addition to matching them for frequency characteristics and temporal structure from visual comparison of spectrograms and waveforms. I statistically verified that there were no significant differences in overall frequency characteristics between the predator and control playlists by conducting paired *t*-tests of four frequency characteristics; peak, maximum, minimum and range (following procedures of Zanette *et al.* 2011). Call length and volume were standardized to an average duration of 2 min and 20 s using Audacity sound file editing software (Audacity 2.1.0 (R); Mazzoni 2015).

The playlists I used during treatments were 60 min long and comprised of each of the 20 exemplars. I assigned a number to each species within the predator treatment and used a random number generator to determine the order of species for each one-hour playlist. Next, I assigned a number to each individual call, and used a random number generator to randomly select calls from each species in turn to create two unique one-hour playlists for each treatment. Playback calls were additionally interspersed with periods of silence (i.e. empty sound files) with an aggregate ratio of 1: 1.5 (calls: silence) following Zanette *et al.* 2011. Furthermore, only one of my three playback units played at any given time and the order in which the units broadcast calls was randomized using a random number generator, ensuring birds did not become habituated to the treatments.

In order to accomplish this, I collected all the exemplars that I could find for all of the species used in my manipulations (see species list in Chapter 2 methods) and then selected the five best examples from those. I then modified these files in Audacity by adding periods of silence at the beginning and ends of the calls in the file so that each file itself had a ratio of 1: 1.5 (calls: silence) without modifying the call pattern itself. I then made sure that I had enough calls to make up a one-hour playlist for each of the treatments. I also made sure that on average the length of each of the calls was not different between species.

Next I organized the playlists themselves using excel, to do this I assigned an individual number from one to 30 to each of the sound files then used the “randbetween” function in excel to determine the order. This provided me with the order in which the calls would be broadcast. The next step was to set up the playlist so that it could be broadcast out of three playback units. To do this I further used the “randbetween”



## Curriculum Vitae

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### EDUCATION

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**Master of Science in Biology** – Western University **2013 – Present**  
 Specialization: Predator effects on prey behaviour and demography  
 Principal investigator: Dr. Liana Zanette

**Bachelor of Science in Biology** – Vancouver Island University **2008 – 2013**  
 Graduated with distinction

### CERTIFICATIONS AND WORKSHOPS

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**Pleasure Craft Operators Licence** **March 2013 – Present**

**Class 5 (Full) Drivers Licence B.C. Canada** **April 2012 – Present**

### RESEARCH & AVIAN EXPERIENCE

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**Graduate Student and Research Assistant** **March 2013 – Present**  
 University of Western Ontario Department of Biology

- Conducted research on how non-consumptive effects of predators effected parental care of a wild population of song sparrows and how these effects were influencing the survival of these same fledglings.
- Conducted daily radio tracking of fledgling song sparrows, the study species, which I am highly proficient at.
- Conducted nest searches for the sparrows locating over 50 nest during the field season.
- Trained field crew members to drive the 12 foot zodiac between island field sites and transporting equipment between sites.
- Assembled portable nest camera set ups hauling car batteries across the field sites.

**Undergraduate Thesis** **August 2011 – April 2012**  
 Department of Biology at Vancouver Island University

- Examined the special variability of soil CO<sub>2</sub> flux and analysed various components of the soil (i.e. chemistry and biota) to predict the variation.

**Research Assistant****December 2012 – March 2013**

Vancouver Island University Banding Station

- Helped to organize and start the banding station with Dr. Eric Demers.
- Cleared mist-net lanes and assembled the nets.
- Instructed volunteers on proper banding and extraction of birds from mist-nets.
- Was the main assistant to Dr. Eric Demers at the station extracting and banding birds.
- Helped to coordinate public displays and demonstrations to the public.

**Research Assistant****April 2012 – April 2013**

Center for Shellfish Research at Vancouver Island University

- Organization of volunteers and their duties. Scheduling the times they could come into the lab, instructing them on jobs that needed to be done, error checking their work and entering it into the main data base.
- I sampled biodiversity on beaches with and without aquaculture.
- Mark recapture of Manila clams (*Venerupis philippinarum*).
- Examining the population dynamics and biological communities associated with the Japanese horn snail (*B.attramentaria*).
- Sediment and water analysis using various probes; DO, pH, Salinity etc.

**Research Assistant****April 2012 – August 2012**

BIOMET at Vancouver Island University

- Collecting soil and Trunk CO<sub>2</sub> efflux measurements as well as photosynthesis measurements with a Licor-6400 photosynthesis system.
- Assisted with the setup of automated trunk respiration chambers and installed root exclusion plots at a field site on the east coast of Vancouver Island.
- Assisted with green roof carbon flux research on green roofs in Nanaimo and Duncan.

**Assistant Raptor Breeder****May 2006 – April 2010**

Hichmough Raptors

- Prepared raptor food and fed birds.
- Incubated and hand reared young hawks and falcons
- Monitored the health and condition of breeding birds.
- Helped with the training of young birds.
- Building pens and general maintenance work at breeding site.

**PUBLICATIONS**

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Dudeck, B., M.C. Allen., M. Clinchy., L. Y. Zanette. (in preparation) *Fear of predators compromises parental care and the survival of post-fledged young in a song bird.*

## **AWARDS & SCHOLARSHIPS**

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<b>Canadian Society of Zoologists Travel Grant.</b> Value = \$500.00	<b>2015</b>
<b>Andy Spencer Legacy Award for achievement in Biology.</b> Value = \$500.00	<b>2013</b>
<b>Western Undergraduate Pre-thesis Award.</b> Value = \$4500.00	<b>2013</b>
<b>Vancouver Island University Dean's List</b>	<b>2012 – 2013</b>

## **MEMBERSHIPS and AFFILIATIONS**

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<b>Animal Behaviour Society</b>	<b>February 2014 – Present</b>
<b>Canadian Society of Zoologists</b>	<b>February 2014 – Present</b>
<b>Ornithological Societies of North America</b>	<b>March 2012 – Present</b>
<b>British Columbia Falconry Association</b>	<b>April 2001 – March 2013</b>
<b>Nanaimo 4-H Poultry Club</b>	<b>February 1998 – September 2010</b>

## **CONFERENCES and PRESENTATIONS**

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May 2015. *Fear of predators compromises parental care and the survival of post-fledged young*, Canadian Society of Zoologists, Calgary AB

May 2015. *Fear of predators compromises parental care and the survival of post-fledged young*, Ontario Ecology, Ethology, and Evolution Colloquium, Toronto ON

October 2014. *Fear of predators compromises parental care and the survival of post-fledged young*, Friday Philosophical Graduate Seminar Series, London, ON

October 2014. *Acute predation threat affects parental provisioning to offspring*, Biology Graduate Research Forum, London ON

## **TEACHING EXPERIENCE**

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### **Graduate Teaching Assistant**

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Department of Biology

- BIO 3446B: Wildlife Ecology 2015
- BIO 3332A: Parasitology 2014
- BIO 1001A: Introductory Biology 2014
- BIO 2290G: Scientific Methods in Biology 2013
- BIO 3440A: Ecology of Populations 2013

### **Undergraduate Teaching Assistant**

Vancouver Island University

Department of Biology

- BIO 329: Vertebrates of British Columbia 2013
- BIO 220: Aquatic Ecology 2012

## **VOLUNTEER EXPERIENCE**

---

**Vancouver Island University Bird Banding Station**

*November 2012 – Present*

**Rocky Point Bird Observatory**

*August 2012 – October 2012*

**Nanaimo 4-H Club**

*2006 – 2012*