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DEVELOPMENTAL, ECOLOGICAL, AND LIFE HISTORY INFLUENCES ON PREDATOR-INDUCED PLASTICITY IN SONGBIRDS

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DEVELOPMENTAL, ECOLOGICAL, AND LIFE HISTORY INFLUENCES ON PREDATOR-INDUCED PLASTICITY IN SONGBIRDS

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ABSTRACT

Predation is a ubiquitous ecological force that plays a major role in the evolution of phenotypes. Where the predation risk is predictable and variable, prey species are expected to evolve plasticity in traits that reduce the likelihood of being killed and eaten by predators. Such plasticity may be especially critical for the survival of dependent offspring because they are particularly vulnerable to predators and suffer high levels of predation across taxa. Yet the fitness effects of predator-induced plasticity can vary across life stages, differ between parents and offspring, or be mediated by interactions with other species in the community. The importance of each of these factors for mediating the fitness consequences of predator-induced plasticity in natural systems is poorly understood. In this dissertation, I explore these issues using experiments and observational data in a suite of songbird species.

In chapter 1, I examine how plastic responses to increased nest predation risk influence offspring morphology, flight performance and survival after they depart the nest as fledglings. When nest predation risk was elevated, young departed the nest with shorter, but more fully feathered wings. Ultimately, plastic responses to increased nest predation risk did not reduce flight performance or survival of young after they departed the nest.

In chapter 2, I test whether parental responses to increased nest predation risk better reflect strategies to mitigate predation risk for offspring or enhance parental fitness at a cost to current offspring. I show evidence that variation in parental responses to increased nest predation risk across species better reflects adjustments in parental effort that maximize parental but not necessarily offspring fitness.

In chapter 3, I explore how species interactions vary with nest predation risk and examine the consequences for offspring survival. I show that in years with higher nest predation risk, cavity nesting birds nested together in individual trees more often and experienced greater offspring survival compared to nests in trees with only one nest.

In chapters 4-5, I examine the potential for parent-offspring communication to influence parental responses to nest predation risk. In songbirds, offspring use conspicuous, loud begging displays to solicit feeding from parents. Consequently, offspring may be able to shape parental responses to nest predation risk to favor offspring over parental fitness. Yet parental responsiveness to begging varies among species and increased offspring begging may exacerbate nest predation risk by helping predators locate nests. In chapter 4, I explore the evolutionary drivers of parental responsiveness to begging by comparing parental responsiveness across species with diverse life history and ecological traits. Parents were more responsive to offspring begging in species with smaller nestlings at greater risk of starvation on average. However, I found less evidence that annual adult survival or nest predation rates drive parental responsiveness to begging. In chapter 5, I examine whether variation in nest structure across species mediates how offspring begging affect nest predation risk. Increased offspring begging cues were associated with higher nest predation rates in enclosed nests (with constructed walls and a roof) but had little impact on nest predation rates in open cup nests. Together, these two studies suggest that offspring may be able to influence parental responses to offspring predation risk in some species and set the stage for more in depth studies of this phenomenon.

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A project of this kind lists one name as the author, but the reality is that this document represents the hard work, dedication, and support of many.

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TABLE OF CONTENTS

INTRODUCTION

Predation is a ubiquitous ecological force that plays a major role in the evolution of traits important for fitness. Where predation risk is predictable and variable, prey species are expected to evolve plasticity in traits that reduce the likelihood of being killed and eaten by predators (Martin and Briskie 2009). Such plasticity may be especially critical for the survival of young offspring because they are particularly vulnerable to predators and suffer high levels of predation across taxa (Eckert 1987; Promislow & Harvey 1990; Gosselin & Qian 1997; Martin et al. 2017). Yet the fitness effects of predator-induced plasticity are not always clear. Plastic responses to offspring predation risk that increase offspring survival early in life may yield survival costs during subsequent life stages (Taborsky 2017). Moreover, parental responses that mitigate predation risk for offspring may reduce lifetime parental fitness (Williams 1966; Law 1979; Michod 1978; Roff 2002; Marshall and Uller 2007; Sheriff & Love 2013). Offspring may also be able to shift the level of parental care in their favor by begging (Trivers 1974; Price 1998; Tarwater 2009; Haff & McGrath 2011). Thus, if parents are responsive to offspring begging cues, parent-offspring communication may have implications for the fitness effects of parental responses to risk (Marshall & Uller 2007; Taborsky 2017). Given the importance of predation as a driver of the evolution of phenotypes, understanding the fitness consequences of predator-induced plasticity is a major goal in ecology and evolution.

Here, I address these issues using experiments and long-term observational data on songbirds from field sites in Arizona, USA and Malaysian Borneo. Songbirds provide a good system for examining parental and offspring responses to predation risk. Among songbirds, nest predation is often the primary source of offspring mortality across species (Nice 1957, Martin 1995, Martin and Briskie 2009). Nest predation risk is temporally and spatially variable and can be detected by birds through auditory cues (e.g. Fontaine and Martin 2006, Zannette et al. 2011; Emmering & Schmidt 2011; Hua et al. 2014) which should favor the evolution of adaptive plasticity to nest predation risk.

This dissertation is organized into two main sections: First, I ask how variation in nest predation risk affects parental care and fitness. Second, I examine whether social interactions between parents and offspring have the potential to limit the expression of adaptive parental responses to nest predation risk.

I. How does nest predation risk shape parental care and fitness?

Plastic responses to predation risk may allow young organisms to reduce mortality from predation, but may yield costs to performance and survival in future life stages (Monaghan 2008; Harrison et al. 2011; Touchon et al. 2013; Taborsky 2017). Yet studies that examine the consequences of plastic responses to predation risk across life stages in natural systems are rare. In chapter 1, I manipulated the perceived risk of predation during the nesting stage and examine the consequences for offspring morphology, locomotor (flight) performance, and survival.

Responses to predation risk need not maximize offspring survival to be adaptive (Roff 2002; Marshall & Uller 2007; Sherriff & Love 2013; Taborsky 2017). Life history theory predicts that parents may maximize their lifetime fitness by reducing care provided to current young when predation risk is high by increasing the probability they survive and reproduce in the future (Law 1979; Michod 1979; Roff 2002). In support of this idea, many studies show that parents feed their young less frequently when predation risk is elevated (Fontaine & Martin 2006; Eggers et al. 2008; Ghalambor & Martin 2001; Ghalambor et al. 2013; Hua et al. 2014; LaManna & Martin 2016). Yet reduced feeding is also thought to increase offspring survival by making it more difficult for predators to locate young (Skutch 1945; Martin et al. 2000; Muchai & DuPleiss 2005). Thus, whether this pattern reflects a response to reduce parental effort to maximize parental fitness or help mitigate risk for current young is unclear. Comparing responses in other parental traits (i.e. egg size, clutch mass, incubation behavior) across species with different life history strategies may help determine whether parental responses to offspring predation risk function to mitigate risk for current young or enhance continued parental survival. In chapter 2, I use playback experiments among species that differ in average nest predation rate and annual adult survival rates to distinguish these two hypotheses.

The fitness consequences of parental responses to predation risk may also be mediated by interactions with other prey species in the community. Ecological theory suggests that the strength and direction of ecological interactions between prey species may vary with the level of predation risk (Bertness & Callaway 1994; Agrawal et al. 2007; Chamberlain et al. 2014). On one hand, apparent competition may become more intense when predation risk is elevated making close interactions between prey more negative and exacerbating fitness costs of risk (Holt 1977; Martin 1988, 1993, 1996). On the other hand, elevated risk may favor more facilitation among species which may help buffer fitness from predation risk impacts (Hamilton 1971; Morse 1977; Bertness & Callaway 1994; Quinn and Ueta 2008). In chapter 3, I use a long-term dataset to examine how interannual variation in predation risk influences nesting associations between species that compete for nesting sites and the implications for these associations for offspring survival.

II. Can parent-offspring interactions influence the fitness and responses to predation risk?

Parents of many taxa are known to adjust the level of care provided to offspring based on offspring solicitation cues (Kilner & Hinde 2008). Begging cues from offspring may help parents to efficiently provide care to offspring (Godfray 1991; Godfray 1995; Grodzinski & Lotem 2007). However, offspring are expected to demand more care than is optimal for parental lifetime fitness (Trivers 1974). If offspring can exert control over parental provisioning, parental responses to predation risk may be limited with implications for both offspring and parental fitness (Taborsky 2017). In some species, offspring have substantial control over parental feeding: when offspring begging cues are more intense parents feed more often (Clark & Lee 1998; Hinde & Kilner 2007; Tarwater et al. 2009; Caro et al. 2016). Yet parents seem not to respond to offspring begging in other species (Price 1998; Haff & Magrath 2011; Caro et al. 2016). The ability of offspring begging to influence the amount of food provided to a current brood of young may vary across species, but tests of this idea are lacking. In chapter 4, I experimentally increase the intensity of offspring begging at nests of 17 species of songbird to examine whether opportunities for future reproduction (i.e. adult survival), average predation risk, offspring size, or food predictability influence parental responsiveness to offspring begging across species.

Offspring begging can also directly exacerbate predation risk by attracting predators (Haskell 1994; Leech & Leonard 1997; Haff & Magrath 2011; Stynoski et al. 2018). Because parents have more knowledge about the presence of predators near the nest at any given time (Kilner & Hinde 2008), offspring may experience fewer benefits and greater costs for influencing parental care by begging as predation risk increases. Yet the extent to which offspring begging attracts predators is unclear and likely varies among species. For example, variation in nest structure may influence the predation costs of begging. Enclosed nests have traditionally been thought to reduce nest predation risk because young are concealed visually and their begging calls may be muffled making more difficult for predators to identify and locate nests (Wallace 1889; Nice 1957; Oniki 1985; Collias 1997; Hall et al. 2015). Yet while protective benefits of enclosed nests are often assumed, strong functional tests of this idea are lacking. In chapter 5, I use experiments along with functional and comparative tests to examine how nest structure influences average nest predation risk and the predation costs of offspring begging.

Parental responses to offspring predation risk are critical for fitness but whether such responses increase parental fitness, offspring fitness, or both is unresolved (Marshall & Uller 2007; Sherriff & Love 2013; Taborsky 2017). Moreover, differences in the ecology and life history strategies between species likely shape responses to risk and their fitness consequences (Law 1979; Michod 1979; Roff 2002; Marshall & Uller 2007; Sherriff & Love 2013; Taborsky 2017). Here, I provide a series of studies that examine the fitness consequences of plastic responses to risk and preliminary work describing how parent-offspring conflict and communication might influence them.

References:

Agrawal, A.A., *et al.* (2007). Filling key gaps in population and community ecology. *Frontiers Ecol. Env*. **5**, 145-152.

Benard, M.F. (2004). Predator-induced phenotypic plasticity in organisms with complex life histories. *Annu. Rev. Ecol. Evol. Syst. **35***, 651-673.

Bertness, M.D. & Callaway, R. (1994). Positive interactions in communities. *Trends Ecol. Evol. **9***, 191-193.

Briskie, J.V., Martin, P.R., & Martin, T.E. (1999). Nest predation and the evolution of nestling begging calls. *Proc. R. Soc. B* **266**, 2153-2159.

Caro, S.M., Griffin, A.S., Hinde, C.A., West, S.A. (2016). Unpredictable environments lead to the evolution of parental neglect in birds. *Nature Comm.* **7**, 10985.

Chamberlain, S.A., Bronstein, J.L. & Rudgers, J. A. (2014). How context dependent are species interactions? *Ecol. Lett.* **17**, 881-890.

Charlesworth, B. (1994). *Evolution in age-structured populations,* Cambridge, UK: Cambridge University Press.

Clark, C.W. (1994). Antipredator behavior and the asset-protection principle. *Behav. Ecol.* ***5,*** 159-170.

Clark, A.B & Lee, W.H. (1998). Red-winged blackbird females fail to increase feeding in response to begging call playbacks. *Anim. Behav.* **56**, 563-570.

Collias, N.E. (1997). On the origin and evolution of nest building by passerine birds. *Condor* **99**, 253–270.

Collias, N.E. & Collias, E.C. (1984). *Nest building and bird behavior*. Princeton University Press, Princeton, NJ, USA.

Creel, S., Christianson, D. (2008). Relationships between direct predation and risk effects. *Trends Ecol. Evol. **23***, 194-201.

Eggers, S., Griesser, M., & Ekman, J. (2008). Predator-induced reductions in nest visitation rates are modified by forest cover and food availability. *Behav. Ecol.* **19**, 1056-1062.

Emmering, Q.C. & Schmidt, K.A. (2011). Nesting songbirds assess spatial heterogeneity of predatory chipmunks by eavesdropping on their vocalizations. *J. Anim. Ecol.* **80**, 1305-1312.

Fontaine, J.J. & Martin, T.E. (2006). Parent birds assess nest predation risk and adjust their reproductive strategies. *Ecol. Lett.* **9**, 428-434.

Ghalambor, C.K. & Martin, T.E. (2001). Fecundity-survival trade-offs and parental risk-taking in birds. *Science **292***, 494-497.

Ghalambor, C.K., McKay, J.K., Carroll, S.P., & Reznick, D.N. (2007). Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. *Func. Ecol. **21***, 394-407.

Ghalambor, C.K., Peluc, S.I., Martin, T.E. (2013). Plasticity of parental care under the risk of predation: how much should parents reduce care? *Biol. Lett.* **9**, 20130154.

Godfray, H.C.J. (1991). Signalling of need by offspring to their parents. *Nature* **352**, 328-330.

Godfray, H.C.J. (1995). Signaling of need between parents and young: parent-offspring conflict and sibling rivalry. *Am. Nat.* **146**, 1-24.

Grodzinski, U. & Lotem, A. (2007). The adaptive value of parental responsiveness to nestling begging. *Proc. R. Soc. B* **274**, 2449-2456.

Haff, T.M. & Magrath, R.D. (2011). Calling at a cost: elevated nestling calling attracts predators to active nests. *Biol. Lett.* **7**, 493-495.

Hall, Z.J., Street, S.E., Auty, S. & Healy, S.D. (2015). The coevolution of building nests on the ground and domed nests in Timaliidae. *Auk* **132**, 584-593.

Hamilton, W.D. (1971). Geometry for the selfish herd. *J. Theor. Biol.* **31**, 295-311.

Harrison, X. A., Blount, J. D., Inger, R., Norris, D. R. & Bearhop, S. (2011). Carry-over effects as drivers of fitness differences in animals. *J Anim Ecol* **80**, 4-18.

Haskell, D.G. (1994). Experimental evidence that nestling begging behavior incurs a cost due to nest predation. *Proc. R. Soc. B* **257**, 161-164.

Haskell, D.G. (2002). Begging behavior and nest predation. In J. Wright & M. L. Leonard (Eds.), *The Evolution of Begging* (pp. 163-172). Dordrecht, The Netherlands: Kluwer Academic Publishers.

Hinde, C.A., & Kilner, R.M. (2006). Negotiations within the family over the supply of parental care. *Proc. R. Soc. B* **274**, 53-60.

Hua, F., Sieving, K.E., Fletcher Jr, R.J., & Wright, C.A. (2014). Increased perception of predation risk to adults and offspring alters avian reproductive strategy and performance. *Behav. Ecol.* **25**, 509-519.

Kilner, R.M. & Hinde, C.A. (2008). Information warfare and parent–offspring conflict. *Adv. St. Behav.* **38**, 283-336.

Law, R. (1979). Optimal life histories under age-specific predation. *Am. Nat.* **114**, 399-417.

LaManna, J.A. & Martin, T.E. (2016). Costs of fear: behavioural and life-history responses to risk and their demographic consequences vary across species. *Ecol. Lett.* **19**, 403-413.

Lima, S.L. & Dill, L.M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool. **68***, 619-640.

Lima, S.L. & Bednekoff, P.A. (1999). Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *Am. Nat.* **6**, 649-659.

Leech, S.M. & Leonard, M.L. (1997). Begging and the risk of predation in nestling birds. *Behav. Ecol.* **8**, 644-646.

Loiselle, B.A. & Hoppes, W.G. (1983). Nest predation in insular and mainland lowland rainforest in Panama. *Condor* **85**, 93-95.

Magrath, R.D., Haff, T.M, Horn, A.G., & Leonard, M.L. (2010). Calling in the face of danger: predation risk and acoustic communication by parent birds and their offspring. *Adv. St. Behav.* **41**, 187-251.

Martin, T.E. (1988). On the advantage of being different: Nest predation and the coexistence of bird species. *PNAS* **85**, 2196-2199.

Martin, T.E. **(**1993). Nest predation and nest sites: New perspectives on old patterns. *BioScience* **43**, 523-532.

Martin, T.E. **(**1995). Avian life history evolution in relation to nest sites, nest predation and food. *Ecol. Monog.* **65**,101-127.

Martin, T. E. (1996). Fitness costs of resource overlap among coexisting bird species. *Nature* **380**, 338-340.

Martin, T.E. & Briskie, J.V. (2009). Predation on dependent offspring: a review of the consequences for mean expression and phenotypic plasticity in avian life history traits. *Ann. NY Acad. Sci.* **1168**, 201-217.

Martin, T.E., Scott, J., & Menge, C. (2000). Nest predation increases with parental activity: separating nest site and parental activity effects. *Proc. R. Soc.* B **267**, 2287-2293.

Martin, T.E., Boyce, A.J., Fierro-Calderon, K., Mitchell, A.E., Armstad, C.E., Mouton, J.C., & Bin Soudi, E.E. (2017). Enclosed nests may provide greater thermal than nest predation benefits compared with open nests across latitudes. *Func. Ecol.* **31**, 1231-1240.

Marshall, D.J., Uller, T. (2007). When is a maternal effect adaptive? *Oikos*, **116**, 1957-1963.

Michod, R.E. (1979). Evolution of life histories in response to age-specific mortality factors. *Am. Nat.* **133**, 531-550.

Monaghan, P. (2007). Early growth conditions, phenotypic development and environmental change. *Phil. Trans. R. Soc. B* **363**, 1635-1645.

Morse, D.H. (1977). Feeding behavior and predator avoidance in heterospecific groups. *Bioscience* **27**, 332-339.

Muchai, M. & Plessis, M.A.D. (2005). Nest predation of grassland bird species increases with parental activity at the nest. *J. Avian Biol.* **36**, 110-116.

Oniki, Y. (1985). Why robin eggs are blue and birds build nests: statistical test for Amazonian birds. *Ornithol. Monog.* **36**, 536-545.

Nice, M.M. (1957). Nesting success in altricial birds. *Auk* **74**, 305-321.

Price, K. (1998). Benefits of begging for yellow-headed blackbird nestlings. *Anim. Behav.* **56**, 571-577.

Price, T.D., Qvarnström, A., & Irwin, D.E. (2003). The role of phenotypic plasticity in driving genetic evolution. *Proc. R. Soc. B* **270**, 1433-1440.

Quinn, J. L. & Ueta, M. (2008). Protective nesting associations in birds. *Ibis* **150**,146-167.

Roff, D.A. (2002). *Life history evolution*. Boston, MA: Springer US.

Sheriff, M.J. & Love, O.P. (2013). Determining the adaptive potential of maternal stress. *Ecol. Lett.* **16**, 271-280.

Skutch, A.F. (1945). Incubation and nesting periods of Central American birds. *Auk* **62**, 8-37.

Snow, D.W. (1978). The nest as a factor determining clutch-size in tropical birds. *J. Ornithol.* **119**, 227-230.

Stynoski, J.L., Stynoski, P.B. & Noble, V.R. (2018). Empirical evidence for multiple costs of begging in poison frog tadpoles. *Zool. Anz.* **273**, 203-209.

Taborsky, B. (2017). Developmental plasticity: preparing for life in a complex world. *Adv. St. Behav.* **49**, 49-99.

Tarwater, C.E., Kelley, J.P. & Brawn, J.D. (2009). Parental response to elevated begging in a high predation, tropical environment. *Anim. Behav.* **78**, 1239-1245.

Touchon, J. C., McCoy, M. W., Vonesh, J. R. & Warkentin, K. M. (2013). Effects of plastic hatching timing carry over through metamorphosis in red-eyed treefrogs. *Ecology* **94**, 850-860.

Trivers, R.L. (1974). Parent-offspring conflict. *Integr. Comp. Biol.* **14**, 249-264.

Wallace, A.R. (1889). *Darwinism*. Project Gutenberg, Urbana, IL, USA, pp. 133-134.

Williams, G.C. (1966). Natural selection, the costs of reproduction, and a refinement of Lack's principle. *Am. Nat.* **100**, 687-690.

Zanette, L.Y., White, A.F., Allen, M.C. & Clinchy, M. (2011). Perceived predation risk reduces the number of offspring songbirds produce per year. *Science* **334**, 1398-1401.

CHAPTER 1: COMPENSATORY PLASTICITY OFFSETS PERFORMANCE AND SURVIVAL COSTS OF PREDATION RISK ACROSS LIFE STAGES.

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Main Text:

Developmental plasticity can help young animals escape predation risk but can also yield costs to performance and survival in subsequent life stages with major implications for lifetime fitness[1-5]. In songbirds, increased nest predation risk favors parents that feed their young less and young that leave their nest (fledge) earlier[4,6-8]. Both responses can result in fledglings with shorter wings, reduced mobility, and decreased survival[4,5,9]. Young may compensate for shorter wings developmentally by increasing feather growth or behaviorally by adjusting flight kinematics or habitat use. Alternatively, underfed young may lack sufficient resources or be too poorly developed to express these compensatory phenotypes[10]. Using experiments and 29 years of observational field data, we show that young from high-risk nests did not leave the nest earlier on average, but growth was slower due to reduced parental feeding. Wings were shorter in high-risk nests when fledglings left the nest early. Yet, young from high-risk nests accelerated the emergence of feathers from their sheaths, which decreased wing porosity and fully compensated for shorter wings, yielding no difference in flight performance relative to young from lower risk nests. Fledglings from high-risk nests also selected safer habitat compared with young from low-risk nests. Together, these developmental and behavioral responses mitigated effects of increased nest predation risk on fledgling survival. Ultimately, our results show that integrated, whole-organism responses to predation risk can evolve to balance tradeoffs in performance and survival across life stages.

Plastic responses to predation risk during development are a common and important way for organisms to increase survival[11-15]. Such plasticity may be especially important in young organisms that are often more vulnerable than other life stages to predation[16-18]. However, plastic responses to predation risk during early life stages can influence phenotypes expressed in later life stages[2,19]. Such carry-over effects may incur fitness costs because selective regimes change throughout ontogeny as young grow in size and move among habitats[1,2,20,21]. In amphibians, plastic responses to predation risk that improve survival during the larval stage can result in reduced locomotor performance after the larval stage (as juveniles), which may increase their subsequent risk of predation[22]. Yet, juveniles may experience neutral or even enhanced juvenile survival when larval predation risk is elevated, suggesting that poor locomotor ability may be compensated by plasticity in other traits[3,23-25]. Thus, while plastic responses to predation risk are often thought to affect performance in later life stages, the implications for fitness in natural environments remain unclear.

Compensatory plasticity in behavioral traits may be especially important for fitness because such traits can rapidly adjust to slow-changing morphological traits and current environmental conditions[26-28]. Grasshoppers reared under chronic predation risk alter jumping kinematics to enhance escape performance despite having similar morphology to grasshoppers from low risk environments[26]. Prey may also increase use of safer habitats that offer protection from predators and increase survival when risk is elevated[27,28]. Still, the ability to express compensatory phenotypes may be limited by resource availability or the developmental state of an organism[10,19]. Ultimately, how morphological and behavioral plasticity interact to influence the fitness consequences of developmental responses to predation risk is poorly understood and studies are critically needed.

In songbirds, a critical life stage transition occurs when young birds depart their nest because mortality is high before and after leaving the nest, but selection pressures can differ dramatically between these stages [4]. High predation rates during the nestling stage select for rapid development and earlier departure from the nest[4,8,15], but high predation during the fledgling stage is thought to favor evolution of young that fledge at older ages with greater mobility[4,5]. Plastic, rather than evolved, responses to increased nest predation risk are also expected to yield earlier nest departure[15]. However, parents plastically reduce feeding rates when nest predation risk is high to reduce the ability of predators to locate nests[13,15], which may limit resources available to young and slow growth of key locomotor traits such as wings[20]. Offspring that leave the nest with shorter wings exhibit poor flight performance as fledglings and may be more susceptible to predators[5,9]. However, young experiencing high nest predation risk could mitigate costs to flight performance by adjusting flight kinematics[27] or accelerating the emergence of flight feathers from the feather sheath to minimize wing porosity[29]. Young from high predation risk environments may also compensate for reduced wing growth by selecting safer, more densely vegetated sites[30]. Yet, it is unclear whether young are physically able to use these compensatory strategies given reduced food resources. Ultimately, tests of the survival consequences of plastic responses to nest predation risk after nest departure are lacking.

Here, we broadcast nest predator calls near nests to increase the perceived risk of nest predation in Dark-eyed Juncos (*Junco hyemalis*) and examined how plastic responses to nest predation risk influence wing morphology, flight performance, habitat selection, and, ultimately, fledgling survival. We augmented our experiment by comparing variation in nest predation rates across years (a continuous proxy for risk), observational data on morphological traits (29 years) and fledgling survival (3 years).

We videoed nests and measured young to examine whether nest predation risk influenced parental care during the nestling period and the wing length of young when they left the nest. We found that parental feeding trips per nestling decreased with experimentally increased perceived predation risk (hereafter treatment; $\beta = -0.373$, $p = 0.038$; Fig. 1a). Fewer feeding trips were associated with slower rates of wing elongation in nestlings from treatment versus control nests (β = -0.027, p = 0.015; Fig. 1b). Despite slower feeding and growth, mean age of young leaving the nest did not differ between treatment vs. control nests (β = 1.186, p = 0.209). Still, fledglings from treatment nests that left the nest early (days 8-10) had shorter wings than fledglings leaving control nests at similar ages (Risk x Age at fledging interaction: β = 1.463, p = 0.040; Fig. 1c). In contrast, fledglings that stayed in the nest until older ages (i.e. days 12-14) had similar wing lengths between treatment and control nests (Fig. 1c).

These results matched patterns from natural variation in risk across years at our site. In years with higher nest predation rates, junco parents reduced feeding rates per nestling (β = -7.786, p = 0.037; Fig. 1d), nestlings increased wing length more slowly (β = -0.372, p = 0.013; Fig. 1e), and did not fledge at younger ages in the long-term dataset (β = 9.343, p = 0.080). Juncos that fledged at relatively earlier ages in higher-risk years left the nest with marginally shorter wings, but juncos that fledged at older ages left the nest with longer wings relative to fledglings from lower-risk years (Risk x Age at fledging interaction: β = 31.709, p = 0.052; Fig. 1f). Thus, while age at nest departure did not differ with nest predation risk on average, nestlings from high-risk nests entered the fledgling stage with shorter wings than birds from safer environments when they left the nest at the early ages favored in risky environments[4,15].

We used 3D videography to measure three flight performance traits: initial acceleration as the bird pushes off a perch, horizontal acceleration in flight, and the ability to maintain a level flight path. Overall, fledglings with longer wings showed greater initial acceleration (β = 0.085, p = 0.044), had marginally higher horizontal acceleration (β = 0.027, p = 0.057), and were better able to stay airborne (β = 0.029, p < 0.001) than fledglings with shorter wings. However, fledglings from treatment nests were better able to maintain a level flight path than fledglings from control nests with similar wing lengths (β = 0.222, p = 0.003; Fig. 2). Compared to fledglings from control nests, fledglings from treatment nests did not achieve this improved flight performance through increased wing beat frequency (β = 0.545, p = 0.659; Extended Data Fig. 1), amplitude (β = -0.011, p = 0.950; Extended Data Fig. 1) or angular velocity (β = 3.391, p = 0.696; Extended Data Fig. 1). However, fledglings from treatment nests exhibited greater emergence of flight feathers (β = 2.532, p = 0.019; Fig. 2) which likely decreased the porosity of their wings and improved net aerodynamic performance[29]. Thus, accelerated emergence of flight feathers compensated for the effects of earlier nest departure and shorter wing length at fledging on flight performance in fledglings from treatment compared with control nests. Nonetheless, birds from both treatment and control nests that fledged at early ages left the nest with shorter wings that yielded substantial costs to flight performance (Fig. 2).

Young leaving the nest early may behaviorally compensate for poor flight performance by selecting safer, more concealed microhabitat than young that leave the nest at later ages. We measured overall vegetation density and density of woody vegetation within 1 meter of fledgling locations for the first three days out of the nest and compared this density to that of random sites within 30m. We found very little support for the idea that fledgling age influenced habitat selection based on overall vegetation density (AICc weight = 0.020; Extended Data Table 1) or woody vegetation density (AICc weight = 0.113; Extended Data Table 2). Moreover, fledglings from treatment nests selected habitat with similar overall vegetation density as fledglings from control nests (AICc weight = 0.808; Fig. 3a; Extended Data Table 1). However, fledglings from treatment nests selected sites surrounded by denser woody vegetation than fledglings from control nests (AICc weight = 0.907; Fig. 3b; Extended Data Table 2). Denser woody vegetation should offer concealment similarly to non-woody vegetation but may also provide a physical barrier that increases protection from predators[30]. Selection for more densely vegetated sites among young from treatment nests could reflect active choice on the part of the young or by parents leading young to particular sites. Nonetheless, fledglings from high-risk treatment nests used habitat that offered more concealment and protection than young from control nests when they were most vulnerable during the first days after leaving the nest.

To examine how experimentally increased nest predation risk influenced fledgling survival, we attached miniature radio transmitters to young in the nest and tracked fledglings for one week after they fledged for experimental and natural nests[5]. We estimated survival rates using Bayesian multistate survival models which accounted for observations where the state (alive or dead) could not always be determined and tested for an effect of fledging age and predation risk. Fledgling survival did not differ between treatment and control nests (β = -0.281; 95% Bayesian CI: -3.23-2.84; Fig. 4a). Fledgling survival from natural nests between two years with relatively low daily nest predation risk (0.032-0.034) did not differ (2014: 0.761, 95% Bayesian CI: 0.457-0.927; 2016: 0.853, 95% Bayesian CI: 0.771-0.911; Fig. 4b). However, fledgling survival during a third year with relatively high daily nest predation risk (0.064) appeared to be greater (2015: 0.969, 95% Bayesian CI: 0.911-0.991; Fig. 4b). Together, these results suggest that increased nest predation risk does not strongly impact fledgling survival, likely reflecting compensatory shifts in habitat selection (Fig. 3b) and flight performance (Fig. 2).

Classic theory suggests that young should transition between life stages earlier when predation risk is elevated[1], but reduced feeding rates or parental care may limit earlier transitions and yield performance and fitness costs in subsequent life stages[2-5]. Our results show that organisms can mitigate such carry-over costs through compensatory plasticity in behavioral and developmental phenotypes. Ultimately, understanding plastic responses to predation risk requires assessment of plasticity in multiple traits and examining fitness consequences across life stages in natural environments.

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References:

1. Case, T. J. On the evolution and adaptive significance of postnatal growth rates in the terrestrial vertebrates. *Q Rev Biol* **53**, 243-282 (1978).
2. Harrison, X. A., Blount, J. D., Inger, R., Norris, D. R. & Bearhop, S. Carry-over effects as drivers of fitness differences in animals. *J Anim Ecol* **80**, 4-18 (2011).
3. Touchon, J. C., McCoy, M. W., Vonesh, J. R. & Warkentin, K. M. Effects of plastic hatching timing carry over through metamorphosis in red-eyed treefrogs. *Ecology* **94**, 850-860 (2013).
4. Martin, T. E. A conceptual framework for clutch-size evolution in songbirds. *Am Nat* **183**, 313-324 (2014).
5. Martin, T. E., Tobalske, B., Riordan, M. M., Case, S. B. & Dial, K. P. Age and performance at fledging is a cause and consequence of juvenile mortality between life stages. *Sci Adv* **4**, eaar1988 (2018).
6. Skutch, A. F. Do tropical birds rear as many young as they can nourish? *Ibis* **91**, 430-458 (1949).
7. Martin. T. E., Scott, J. & Menge, C. Nest predation increases with parental activity: separating nest site and parental activity effects. *Proc R Soc B Lond* **267**, 2287-2293 (2000).
8. Martin. T. E. Avian life history evolution in relation to nest sites, nest predation, and food. *Ecol Monogr* **65**, 101-127 (1995).

9. Jones, T. M., Ward, M.P., Benson, T. J. & Brawn J. D. Variation in nestling body condition and wing development predict cause-specific mortality in fledgling Dickcissels. *J Avian Biol* **48**, 439-447 (2017).
10. Snell-Rood, E. C., Swanson, E. M., Young, R. L. Life history as a constraint on plasticity: developmental timing is correlated with phenotypic variation in birds. *Heredity* **115**, 379-388 (2015).
11. Spitze, K. Predator-mediated plasticity of prey life history and morphology: *Chaoborus americanus* predation on Daphnia pulex. *Am Nat* **139**, 229-247 (1992).
12. Gosline, A. K. & Rodd, F. H. Predator-induced plasticity in guppy (Poecilia reticulata) life history traits. *Aquat Ecol* **42**, 693-699 (2008).
13. Fontaine, J. J. & Martin, T. E. Parent birds assess nest predation risk and adjust their reproductive strategies. *Ecol Lett* **9**, 428-434 (2006).
14. Creel, S. & Christianson, D. Relationships between direct predation and risk effects. *Trends Ecol Evol* **23**, 194-201 (2008).
15. Martin, T. E. & Briskie, J. V. Predation on dependent offspring. *Ann NY Acad Sci* **1168**, 201-217 (2009).
16. Gosselin, L. A. & Qian, P. Y. Juvenile mortality in benthic marine invertebrates. *Mar Ecol Prog Ser* **146**, 265-282 (1997).
17. Promislow, D. E. & Harvey, P. H. Living fast and dying young: A comparative analysis of life-history variation among mammals. *J Zool* **220**, 417-437 (1990).
18. Martin, T. E. Breeding productivity considerations: What are the appropriate habitat features for management? In *Ecology and Conservation of Neotropical Migrants*. (eds Hagan, J. M. & Johnston, D. W), 455-473 (Smithsonian Institution Press, 1992).
19. DeWitt, T. J., Sih, A. & Wilson, D. S. Costs and limits of phenotypic plasticity. *Trends Ecol Evol* **13**, 77–81 (1998).
20. Mainwaring, M. C., & Hartley, I. R. Causes and consequences of differential growth in birds: A behavioral perspective. *Adv St Behav*, **44**, 225-227 (2012).
21. Werner, E. E. & Gilliam, J. F. The ontogenetic niche and species interactions in size-structured populations. *Ann Rev Ecol Syst* **15**, 393-425 (1984).
22. Stamper, C. E., Downie, J. R., Stevens, D. J. & Monaghan, P. The effects of perceived predation risk on pre-and post-metamorphic phenotypes in the common frog. *J Zool* **277**, 205-213 (2009).
23. Relyea, R. A. The lasting effects of adaptive plasticity: predator-induced tadpoles become long-legged frogs. *Ecology* **82**, 1947-1955 (2001).
24. Vonesh, J. R. & Osenberg, C. W. Multi-predator effects across life-history stages: non-additivity of egg-and larval- stage predation in an African treefrog. *Ecol Lett* **6**, 503-508 (2003).
25. Vonesh, J. R. Egg predation and predator-induced hatching plasticity in the African reed frog, *Hyperolius spinigularis*. *Oikos* **110**, 241-252 (2005).
26. Hawlena, D., Kress, H., Dufrensne, E. R. & Schmitz, O. J. Grasshoppers alter jumping biomechanics to enhance escape performance under chronic risk of spider predation. *Funct Ecol* **25**, 279-288 (2011).
27. Werner, E.E., Gilliam, J.F., Hall, D.J. & Mittelbach, G.G. An experimental test of the effects of predation risk on habitat use in fish. *Ecology* **64**, 1540-1548 (1983).
28. Creel, S., Winnie, J., Maxwell, B., Hamlin, K. & Creel, M. Elk alter habitat selection as an antipredator response to wolves. *Ecology* **86**, 3387-3397 (2005).
29. Dial, T. R., Heers, A. M., & Tobalske, B. W. Ontogeny of aerodynamics in mallards: comparative performance and developmental implications. *J. Exp. Biol.* **215**, 3693-3702 (2012).
30. King, D. I., Degraaf, R. M., Smith, M. L. & Buonaccorsi, J. P. Habitat selection and habitat-specific survival of fledgling ovenbirds (*Seiurus* aurocapilla). *J Zool* **269**, 414-421 (2006).

Figure legends:

Fig. 1: Parents fed each nestling less often in high nest predation risk environments in both (a) experimental versus control nests and, (d) across years with naturally variable nest predation risk. Reduced feeding in high-risk nests slowed wing growth rates and affected wing length at fledging in both experimental versus control nests (b,c) and across years with naturally variable nest predation risk (e,f). Elevated nest predation risk yielded nestlings that left the nest with shorter wings if they fledged at early ages. In contrast, if young from high nest predation risk nests fledged at older ages they had similar or longer wings. Solid black lines depict control or low-risk natural nests and dashed red lines depict treatment or high-risk natural nests. Figures depicting natural variation in nest predation risk, show model predictions for years with the maximum (red, dashed) and minimum (black, solid) observed annual predation rates in our data. Error bars and shaded areas depict standard error.

Fig 2: (a) Fledglings from experimental high predation risk nests were better able to support body weight and therefore maintain a level flight trajectory compared with fledglings from control nests for a given wing length. (b) This allowed fledglings from experimental high-risk nests with relatively short wings to fly as well as fledglings with longer wings from control nests that left the nest at the same age. Regardless of treatment, wing length was generally important for flight performance such that (c) fledglings with longer wings stayed relatively level while flying away while (d) fledglings with short wings were often able to maintain level, sustained flight. (e) Fledglings from treatment nests had more developed flight feathers than fledglings from control nests with similar wing lengths. (f) Wing area increases both with wing length (Green arrows) and as flight feathers break out of their sheaths during development (Orange arrows). Solid black lines depict low-risk nests and dashed red lines depict high-risk nests. Shaded areas indicate standard error.

Fig. 3: Fledglings from high-risk treatment nests (a) selected microhabitat sites with similar overall vegetative cover, but (b) selected sites with increased woody cover more than fledglings from control nests. Solid black lines depict control nests and dashed red lines depict treatment nests. Shaded areas depict 95% confidence intervals. Figures are based on the highest supported models with depicted interactions.

Fig. 4: (a) Fledgling survival was similar between high-risk treatment and control nests and (b) in natural nests across years that differ in nest predation risk. Black lines depict low-risk nests/years and red lines depict high-risk nests/years. Dark shaded areas indicate 50% Bayesian credible intervals and light shaded areas indicate 95% Bayesian credible intervals.

Figures:

Fig. 1:

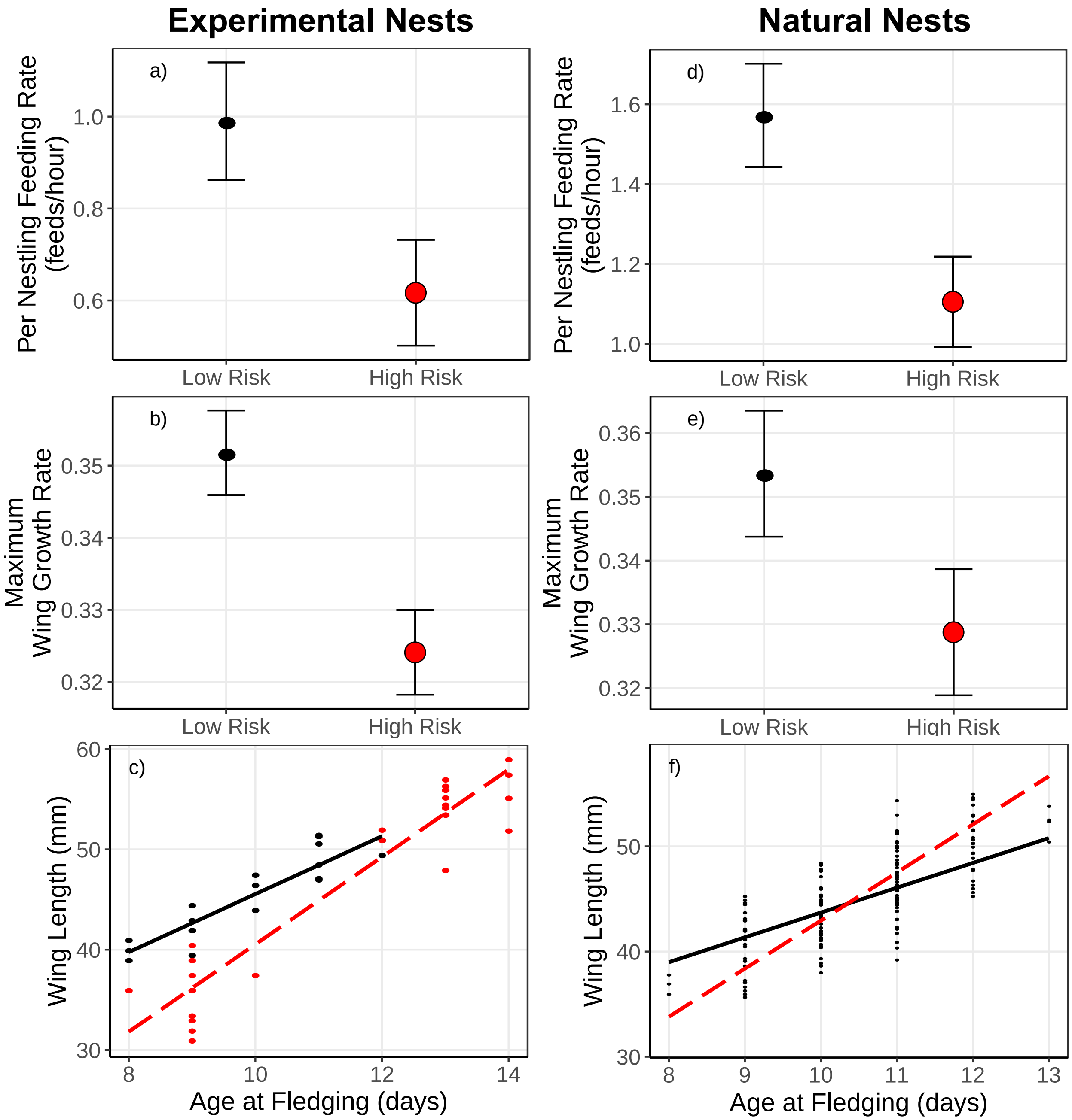


Fig. 2:

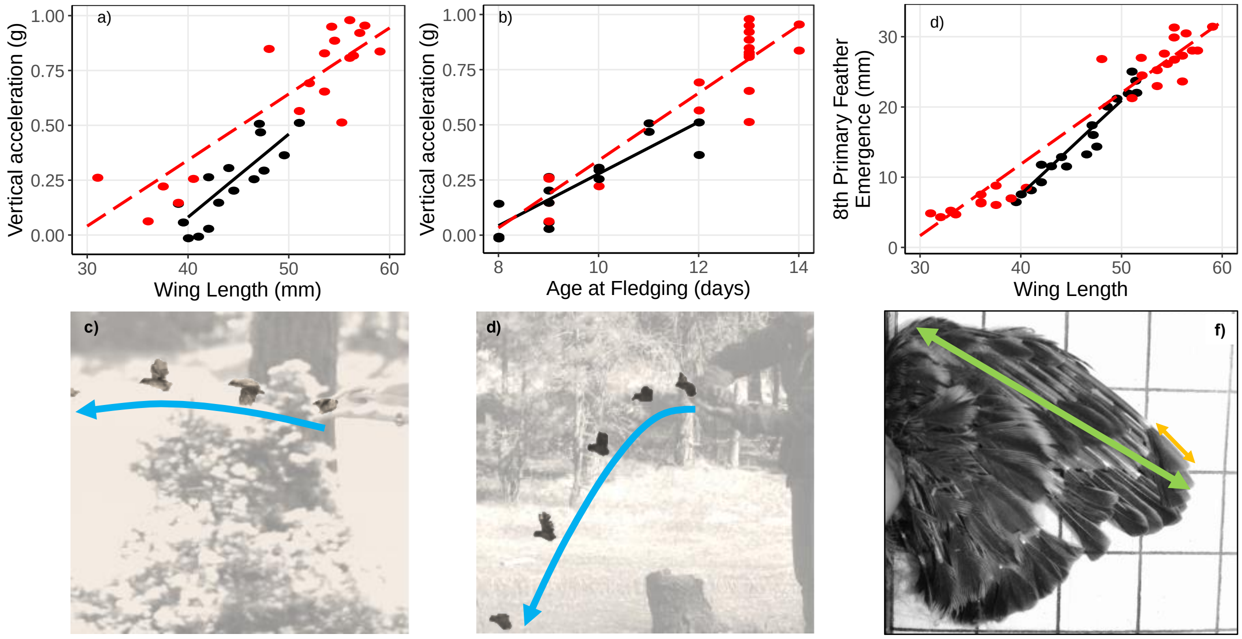

a)
Vertical acceleration (g)
1.00
0.75
0.50
0.25
0.00
30
40
50
60
Wing Length (mm)
b)
Vertical acceleration (g)
1.00
0.75
0.50
0.25
0.00
8
10
12
14
Age at Fledging (days)
d)
8th Primary Feather Emergence (mm)
30
20
10
0
30
40
50
60
Wing Length
c)
d)
f)

Fig. 3:

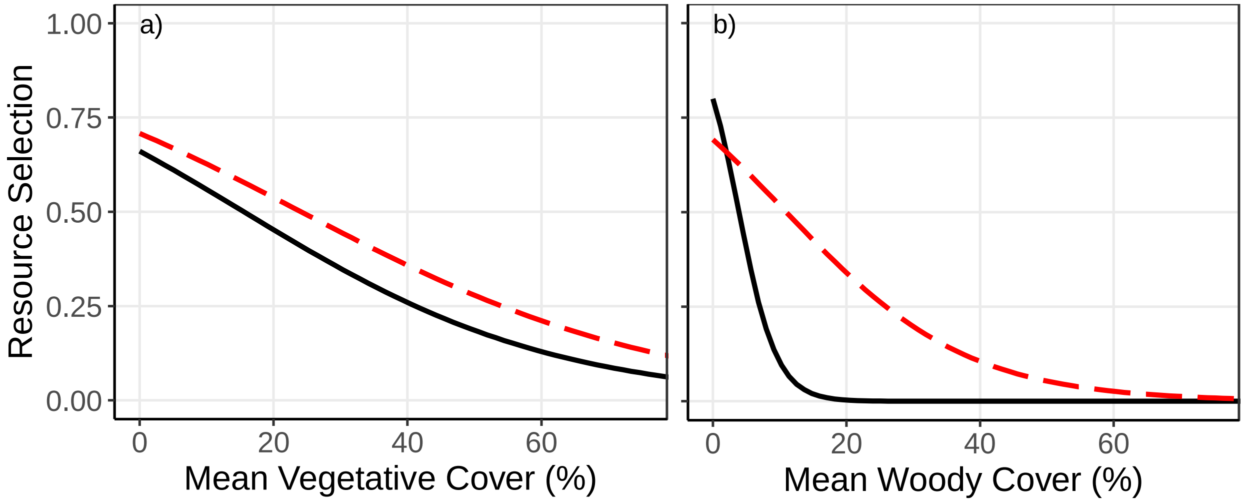
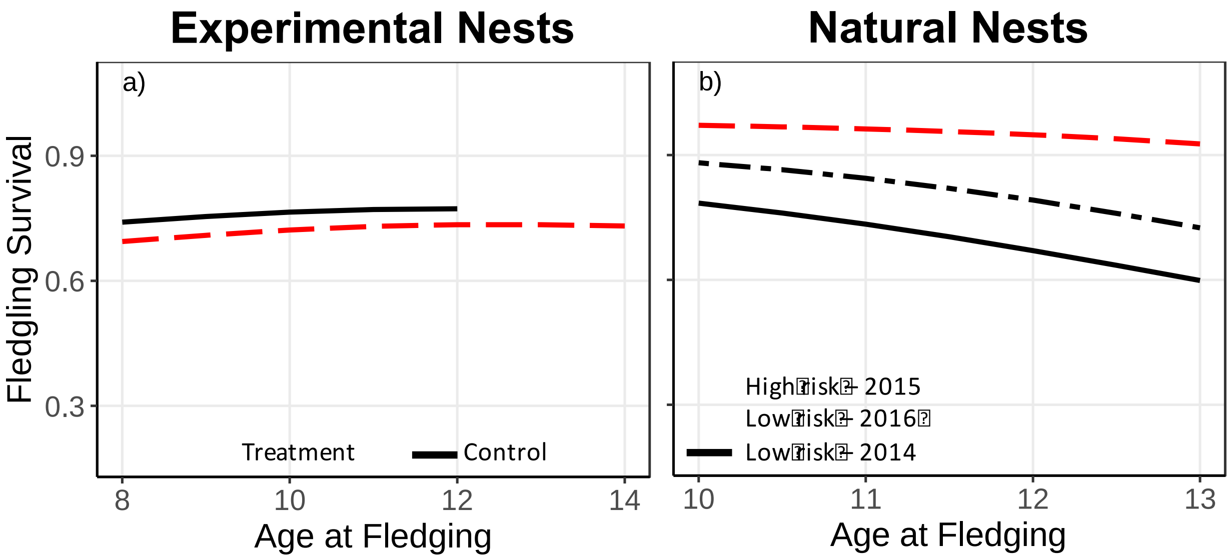

Resource Selection
1.00
0.75
0.50
0.25
0.00
a)
0
20
40
60
Mean Vegetative Cover (%)
b)
0
20
40
60
Mean Woody Cover (%)

Fig. 4:


Experimental Nests
Natural Nests
a)
b)
Fledgling Survival
0.9
0.6
0.3
Treatment
Control
8
10
12
14
Age at Fledging
High risk - 2015
Low risk - 2016
Low risk - 2014
10
11
12
13
Age at Fledging

Materials and Methods:

Study Area:

This study took place between 1987 and 2017 in a mid-elevation (2350 m) mixed deciduous-coniferous woodland in north central Arizona, USA.

Experimental Manipulation of Perceived Nest Predation Risk:

We used a playback experiment to manipulate the perceived risk of nest predation at Dark-eyed Junco nests from 2014 – 2017. We placed three speakers (Eco Extreme by Grace Digital, San Diego, CA, USA) attached to MP3 players (Sansa Clip by San Disk, Milpitas, CA, USA) 4-7 meters from each nest and played the vocalizations of either the red squirrel (*Tamiasciurus hudsonicus*; a common nest predator) or the Western Tanager (*Piranga ludoviciana;* a common songbird that does not compete with Dark-eyed Juncos). We set up speakers two out of every three days at around 0600 and stopped the playback 6 hours later. Each MP3 player was loaded with playlists of 1 minute tracks that played randomly such that the speakers played 11 minutes of silence for every minute of vocalizations. This produced an effect that increased the amount of predator vocalizations heard near a nest site while minimizing the likelihood the Juncos would become accustomed or acclimated to the experiment.

Data Collection:

We found nests of all the ground nesting songbird species at our site (Orange-crowned Warbler (*Vermivora celata*), Red-faced Warbler (*Cardellina rubifrons*), Virginia Warbler (*Leiothlpis virginiae*), and Dark-eyed Junco (*Junco hyemalis*)) from approximately 30 April until 25 July each year by following parents or systematically searching likely nest sites. Nests were monitored every 2-4 days to determine when nests failed and more frequently when transitions between life stages (i.e. eggs hatching, nestlings fledging) were expected.

Nests were filmed periodically using Hi-8 video cameras for 4-6 hours starting at approximately 0600. Films were analyzed to obtain feeding rates per nestling (feeding trips per hour/brood size). Starting in 1999, we measured the wing chord length of nestlings every other day throughout the nestling period. From 2007-2016, we measured nestlings for the first three days after hatch and then every other day until they fledged. In 2017, we only measured nestlings from experimental nests on the day they hatched and on the first day they were found after fledging in order to prevent premature fledging.

In 2017, we studied fledgling habitat selection and survival by attaching miniature radio transmitters (DBA Blackburn Transmitters, Nacogdoches, TX, USA) to the nestlings from experimental nests on the day after their primary feathers broke through their sheaths (usually 8 days after hatching). Transmitters weighed 0.39g and were attached with a figure-8 elastic leg harness that secured the transmitter on the birds lower back. We used a small piece of felt on the underside of the transmitter to prevent damage to feathers and allow a proper fit. After fledging, each nestling was tracked using VHF antennas (RA14-K VHF antenna, TR5 receiver, Teleonics, Mesa, AZ) for 7 days. After the first 7 days, survival rates plateau for this species (TEM *unpubl. data*). Each day, the fledgling's location and survival status (Alive, Dead, Unknown) was recorded. On the first day outside of the nest, we caught all fledglings, measured wing length and the length of the 8th primary flight feather, made 3D films of the fledglings flying (see below), and then returned the fledgling to the location it was caught.

In 2016 and 2017, we made short 3D films of fledglings from experimental nests in flight by simultaneously using two HD video cameras (Hero3+ Black, GoPro, Inc.). The cameras filmed at 120 frames per second and were attached to each end of a 1m long aluminum rod. Fledglings were released facing perpendicular to the view of the cameras and a visual cue (e.g. a person clapping their hands together) was used to ensure the timing of both cameras could be aligned during video analyses. We filmed calibration videos for the two cameras frequently throughout the field season to ensure we could obtain accurate acceleration estimates even if the relative position of the cameras were inadvertently adjusted during the field season.

After the 7-day fledgling tracking period was complete, we measured vegetation density at the locations each fledgling was found during the first three days of tracking. We used a modified profile-board method to assess the density of woody vegetation within 1m of a fledgling's location. We painted eight 0.25 x 0.25m squares on a 2 x 0.25m board in alternating bright colors. This board was placed vertically at the fledgling's location and faced in a random direction. The overall percentage of each square covered by vegetation and the percentage covered by woody vegetation alone was recorded within 1m meter of each fledgling location. The board was rotated 90º to the right, and the same measurements were taken for each square again. The percentage of all squares was then averaged and used in subsequent analyses. Vegetation measurements were taken at each fledgling location and at an associated random site within 25m. To account for changes in vegetation density over time, we assessed vegetation throughout the breeding season.

Data Analysis:

We used linear mixed models to test for an effect of nest predation risk on per-nestling feeding rates. We included days since the eggs hatched and a proxy for nest predation risk as fixed effects and a unique identifier for each nest as a random effect. For the experimental dataset, nest predation risk was a categorical variable for either high-risk treatment or control. For the correlative dataset, we used mean annual nest predation rates of four common ground nesting species (see above) at our site as our proxy for general nest predation risk of our study species, which was a ground-nester. We estimated mean annual nest predation rates using a logistic exposure model with year as a fixed effect and species as a random effect[31]. We used these annual estimates as a continuous variable in all subsequent analyses of natural nests.

We examined the effect of nest predation risk on wing growth rates using non-linear mixed models and the logistic function[32]. First, we determined whether a logistic model fixing the asymptote (A) at 70% of adult size, at 100% of the adult size, or estimating A from the data produced a better fit (lower AIC) for each dataset. The experimental data fits best with A fixed at 70% of adult size and the long term dataset fit best when A was estimated from the data. We then extended the logistic function to include fixed effects that explicitly tested for effects of nest predation risk on all model parameters (A, K: the maximum growth rate and Ti: the time of maximum growth)[32]. We ran models with every possible combination of random effect structure and made inference based on the model with the lowest AIC[32,33].

We used linear mixed models to test for effects of nest predation risk on fledging age, fledgling wing length, flight feather development and all measures of flight performance and flight mechanics. We included a random effect grouping young from the same nest and initially included an interaction between nest predation risk and age at fledging. The interaction term was removed from the model if it was not supported.

We analyzed all 3D films using packages DLTdv5.m[34] and easyWand5.m in program Matlab (R2016a, Mathworks, Inc.). First, we created and tested calibration files against a known acceleration (an object falling at $9.8 m/s^2$) to ensure that the acceleration due to gravity could be calculated within 20%. To calculate flight performance, we digitized a fixed point on each fledgling in each frame from the moment it first made a movement to take off until it was no longer visible. We noted in each film the last frame that the toes of the bird were in contact with any surface as this is the time when the legs stop contributing to the bird's acceleration. We then calculated 3 flight performance measures: initial acceleration as the bird pushes off a perch (3D acceleration until the toes were no longer touching), 2D horizontal acceleration in flight (acceleration in the XY plane after the toes were no longer touching), and the ability to overcome gravity to remain airborne (proportion of vertical acceleration due to gravity after the toes were no longer touching). For each fledgling, we calculated Euclidean distance moved and velocity between each frame and used linear regression to estimate acceleration. To calculate our measures of flight mechanics (angular velocity and amplitude), we digitized points corresponding to the shoulder and the tip of the wing at the top and bottom of the first wingbeat after the toes were no longer in contact. We calculated the angle between these two vectors and the angular velocity in R[35]. We counted the number of frames for each wingbeat on each video and multiplied by the frame rate (120/s) to calculate wingbeat frequency.

We used resource selection models to test whether nest predation risk affected whether habitat selection. Since traditional hypothesis testing using P-values is problematic for logit models with interactions terms[36], we chose to use an information-theoretic approach based on Aikake's Information Criterion for small sample sizes (AICc). Because habitat selection may be influenced by parents and thus be similar among nest mates, we first tested between a full model including a random effect for nest and another full model without random effects[33]. Variance estimates were essentially zero for the model with random effects and the model without random effects was better supported (AIC weight = 0.806), so we did not consider random effects in subsequent analyses. We then tested among candidate generalized linear models including interactions with either woody or overall vegetation density, nestling period length (i.e. age at fledging), and age since fledging.

We used a Bayesian hierarchical multistate survival model to estimate the effect of nest predation risk on fledgling survival. For both the experimental and natural datasets, we modeled the true state of individual i on day t (either alive or dead) conditional on the state in the previous day using a categorical random variable. We fixed transition probabilities between true states such that transitions from dead to alive were impossible. We modeled true state transition from alive to alive (i.e. survival) using a logit model estimating the effects of age at fledging and nest predation risk (experimental data) or year (natural nests). We also included a random effect to account for possible non-independence in survival between fledglings from the same nest. We modeled the observed state of individual i on day t (either alive, dead or unknown) conditional on the individual's true state on that day and our detection probability using a second categorical random variable. We estimated separate detection probabilities for alive and dead birds and fixed the probability of detecting a bird in a state not matching its true state as zero. We used priors with uniform distributions for all parameters except we used a beta distribution for the detection probability for dead birds in the model for experimental data. We parameterized this data based on the posterior distribution from the model of natural nests. We ran three MCMC chains for 100,000 iterations each, retained 20% of samples drawn, and discarded the samples from the first 10,000 iterations. We checked for convergence of chains for all parameters visually using trace plots.

Methods Only References:

31. Shaffer, T. L. A unified approach to analyzing nest success. *Auk* **121**, 526-540 (2004).
32. Sofaer, H. R., Chapman, P. L., Sillet, T. S. & Ghalambor, C. K. Advantages of nonlinear mixed models for fitting growth curves. *J Av Biol* **44**, 469-478 (2013).
33. Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. *Mixed effects models and extensions in ecology with R*. Springer Science & Business Media. (2009).
34. Hendrick, T. L. Software techniques for two- and three-dimensional kinematic measurements of biological and biomimetic systems. *Bioinspir Biomim* **3**, 034001 (2008).

35. R Core Tem. A language and environment for statistical computing. R Foundation for statistical computing, Vienna, Austria. https://www.R-project.org (2017).
36. Berry, W. D., DeMeritt, J. H. R., & Esarey, J. Testing for interaction in binary logit and probit models: is a product term essential? *Am J Pol Sci* **54**, 248–266 (2010).

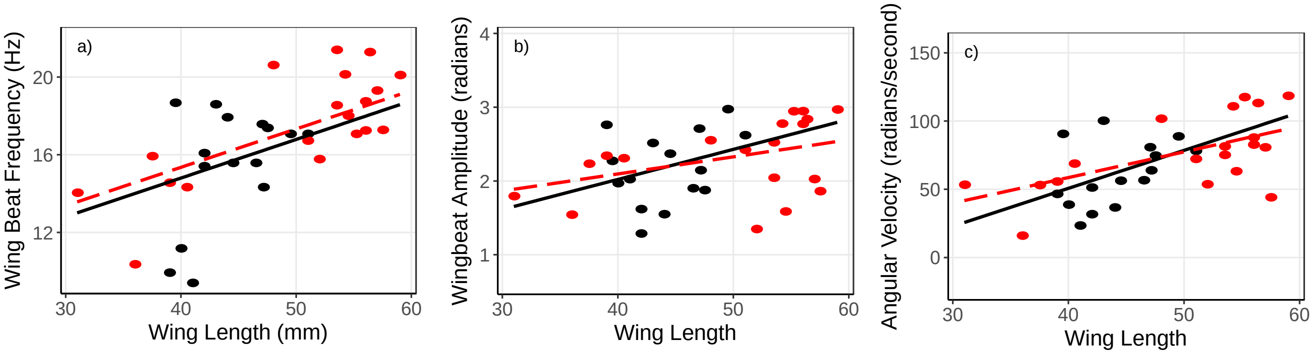
Supplementary Materials:

Extended Data Table 1: AIC table for overall vegetation density resource selection models.

	Age X Veg	Nestling Period X Veg	Risk X Veg	Risk X Nestling Period	Risk X Veg X Nestling Period	df	logLik	AICc	delta	weight
Null						2	-79.5	163.3	0	0.808
Model 6			+			4	-79.2	166.8	3.54	0.138
Model 5		-0.3613	+			6	-79.0	170.7	7.48	0.019
Model 4	-0.310			+		6	-79.1	171	7.77	0.017
Model 2		2.672	+	+	+	8	-77.0	171	8.08	0.014
Model 3	-0.231	-0.3473	+			8	-78.9	175.2	11.91	0.002
Model 1	-0.176	2.642	+	+	+	10	-76.9	175.9	12.66	0.001

Extended Data Table 2: AIC table for woody vegetation density resource selection models.

	Age X Wood	Nestling Period X Wood	Risk X Wood	Risk X Nestling Period	Risk X Wood X Nestling Period	df	logLik	AICc	delta	weight
Model 6			+			4	-67.8	144	0	0.668
Model 5		-0.7464	+			6	-67.4	147.7	3.73	0.104
Model 4	-1.23		+			6	-67.5	147.9	3.89	0.095
Null						2	-71.9	147.9	3.94	0.093
Model 2		-3.533	+	+	+	8	-66.7	150.8	6.81	0.022
Model 3	-1.38	-0.8346	+			8	-67.2	151.7	7.77	0.014
Model 1	-1.63	-5.353	+	+	+	10	-66.3	154.6	10.59	0.004



Extended Data Fig. 1: Neither wingbeat frequency (a), nor amplitude (b), nor angular velocity (c) explained improved flight performance in fledglings from high nest predation risk nests. Solid black lines depict predicted values for low-risk nests and dashed red lines depict high-risk nests. Shaded areas indicate standard errors.

CHAPTER 2: PARENTAL RESPONSES TO OFFSPRING PREDATION RISK ARE INFLUENCED BY ADULT SURVIVAL RATES ACROSS SPECIES.

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Abstract:

Parental responses to variation in offspring predation risk can have major implications for offspring survival. Parental responses to increased predation risk are generally thought to buffer vulnerable offspring from predation risk and increase their chances of survival. Species with greater average predation rates may respond more strongly to protect young from risk. Yet life history theory predicts that parents should reduce parental effort when offspring predation risk is elevated which may instead exacerbate predation risk for offspring. In this case, longer-lived species with more opportunity to reproduce in the future should reduce parental effort to a greater degree than short-lived species when offspring predation risk is high. Here we broadcast nest predator calls near nests of 2 short-lived, low nest predation cavity nesting and 2 longer-lived, high nest predation ground nesting songbirds and examined responses in parental care. Short-lived cavity nesting species responded to increased predation risk by increasing parental effort. In contrast, longer-lived ground nesting species generally responded by reducing parental effort. Ultimately, our results suggest that parental care responses to predation risk are shaped by variation in reproductive value rather than average predation risk.

Keywords: nest predation risk, developmental plasticity, parental effects, life history, residual reproductive value, non-consumptive effects

Introduction:

Predation is a major source of mortality for offspring across taxa with important implications for fitness and population dynamics (Eckert 1987; Promislow & Harvey 1990; Gosselin & Qian 1997; Martin et al. 2017). When the risk of predation is variable and predictable, parents are expected to evolve plastic responses in parental care to increased risk that reduce the chances of their offspring being killed and eaten (Lima & Dill 1990; Benard 2004; Creel & Christianson 2008; Martin & Briskie 2009). Such adaptive responses may reduce exposure of offspring to predation risk or help shape offspring phenotypes for survival in high predation environments (*risk mitigation hypothesis*; Marshall & Uller 2007; Coslovsky & Richner 2011; Giesing et al. 2011). However, life history theory predicts parents should reduce expenditure on current offspring when offspring predation risk is elevated to increase their chances of producing more offspring in the future when predation may be lower (*reproductive value hypothesis*; Law 1979; Clark 1994; Marshall & Uller 2007; Sheriff & Love 2013). Ultimately, whether parents adjust care in high predation environments to increase offspring survival or reduce effort to save energy for the future is unclear. Distinguishing between these alternatives is critical for understanding the function, consequences, and evolution of predator-induced plasticity in parental care.

If parental responses to offspring predation risk primarily function to buffer young from predation risk (*risk mitigation hypothesis*), species with higher average offspring predation rates should adjust parental care traits in ways that improve offspring survival to a greater extent than species with low mean predation rates. In contrast, if parental responses to offspring predation risk function primarily to increase parental fitness in the long term (*reproductive value hypothesis*), species with more opportunity to reproduce in the future (i.e. higher adult survival) should reduce reproductive effort when offspring predation risk is high to a greater degree than species with few opportunities to reproduce in the future (i.e. lower adult survival; Gadgil & Bossert 1970; Michod 1979; Clark 1994). Short-lived species, with little chance of reproducing in the future, may even respond to nest predation risk by increasing parental effort and buffering young from risk. Such responses may cause offspring of longer-lived species to be more vulnerable to increased predation risk relative to shorter lived species.

Songbirds provide a good system for addressing these issues because species vary in adult survival and offspring predation rates and parents are known to detect predator cues and adjust parental care traits when predation risk for eggs and young in the nest is elevated. Furthermore, the benefits and costs of various parental care traits are well understood (Martin & Briskie 2009). For example, increased investment in total egg mass (i.e. clutch mass) and incubation (i.e. warming the eggs in the nest) can reduce survival and future reproduction in parents (Reid et al. 2000; Monaghan et al. 2001; Nager et al. 2001; Visser & Lessells 2001). On the other hand, larger egg mass is associated with higher quality offspring and can increase offspring fitness (Krist 2011). Moreover, warmer egg temperatures yield faster development and increase offspring quality and survival (DuRant et al. 2012; Hepp & Kennamer 2012; Ton & Martin 2017). Faster development is especially important for avoiding nest predation risk because the longer young stay in the nest the more likely a predator is to find and depredate the nest (Martin & Briskie 2009). Thus, parental responses to maximize adult survival and future reproduction should be characterized by reductions in clutch mass and incubation attentiveness, and increases in incubation period length (Fig. 1A). In contrast, responses that favor survival of current young should include increased egg mass and incubation attentiveness, and decreases in incubation length (Fig. 1B). Here we use an experiment to examine whether responses to increases in perceived nest predation risk better reflect decreased parental effort or strategies to improve offspring survival in high risk environments.

Study Area and Methods:

Study species and data collection:

We studied 4 species of songbird in Coconino National Forest in central Arizona, USA (~34° N) at about 2350 m elevation in mixed deciduous and coniferous forest (Table 1). We chose two cavity nesting species that are characterized by similarly low nest predation rates and low annual adult survival to compare with two species that nest in open cups on the ground and experience similarly high nest predation rates and high annual adult survival (Table 1; Martin et al. 2015). We searched for nests daily between May-July from 2014-2017. Nests were monitored every 2-4 days to determine nest success rates and more often near life-stage transitions (e.g. egg laying, eggs hatching). Eggs were weighed within the first 2 days of being laid using a digital scale (Gem-Pro 250, ± 0.001 g). We assessed incubation attentiveness by either filming nests between 0500-1300 or hiding a small temperature probe in the lining of the nest cup which logged temperature readings of the nest every 12 seconds (HOBO Stowaway, Onset Computer, Bourne, MA).

Playback Experiment:

We used a playback experiment to manipulate the perceived risk of nest predation at nests of each study species from 2014 – 2017. We placed three speakers (Eco Extreme by Grace Digital, San Diego, CA, USA) attached to MP3 players (Sansa Clip by San Disk, Milpitas, CA, USA) about 4-7m from each nest and played vocalizations of either red squirrels (*Tamiasciurus* *hudsonicus*; a common nest predator) or Western Tanagers (*Piranga ludoviciana*; a control). Red squirrels depredate nests of all study species as they can gain access to cavity nests by chewing to enlarge the nest entrance (Fontaine & Martin 2006). We set up speakers two of every three days at around 0600 and stopped the playback 6 hours later. Each MP3 player was loaded with playlists of 1 minute tracks that played randomly such that the speakers played 11 minute of silence for every minute of vocalizations.

Statistical Analyses:

We used linear mixed-models to test for an interaction between the effect of increased nest predation risk on egg mass, clutch mass, incubation attentiveness, and incubation period and the type of species (cavity vs. ground nesters). Models for egg mass and incubation attentiveness included fixed covariates for clutch size and the day of the incubation period, respectively. Models for incubation period included a covariate for the date incubation began. To control for repeated measures, we included a random effect for species in all models and another for each nest (except in clutch mass and incubation period models). All dependent variables were standardized to allow comparisons between species.

Results:

Responses to experimental predator playback differed for each trait and varied across species (Fig. 2). Species with low adult survival and low nest predation rates (cavity nesting) showed greater increases in egg mass ($\beta = 0.015$, $P < 0.001$; Fig. 2A) and greater increases in clutch mass ($\beta = 0.077$, $P = 0.053$; Fig. 2B), and incubation attentiveness ($\beta = 0.834$, $P = 0.039$; Fig. 2C) compared with species with high adult survival and high nest predation rates (ground nesting). Incubation periods did not differ significantly in any species. However, incubation periods tended to shorten with increased predation risk in cavity nesting species and lengthen in ground nesting species (Fig. 2D), but this pattern was not significant (β = -0.350, P = 0.445).

Discussion:

Plastic responses to predation risk are typically thought to reduce the likelihood of being depredated (*risk mitigation hypothesis;* Lima & Dill 1990; Benard 2004; Creel & Christianson 2008; Martin & Briskie 2009). Yet parental responses to predation risk may instead maximize lifetime fitness without reducing mortality risk to current offspring (*reproductive value hypothesis;* Law 1979; Clark 1994; Marshall & Uller 2007; Sheriff & Love 2013). We found that shorter-lived cavity nesting species generally showed greater increases in parental effort with increased nest predation risk than longer-lived ground nesting species (Fig. 2). We did not observe a statistically significant difference in the effect of nest predation risk on incubation period length among cavity vs. ground nesting species. Still, on average, incubation periods decreased in cavity nesters and slightly increased in ground nesters (Fig. 2D). Thus, consistent with the *reproductive value hypothesis*, short-lived species responded to predation risk by increasing parental effort to buffer young from risk, while long-lived species reduced parental effort to enhance future reproduction.

Previous work has provided mixed evidence for the *reproductive value hypothesis*. In higher risk habitat, songbirds with multiple opportunities to breed in a season reduced overall investment in egg mass while single brooded species increased egg mass (LaManna & Martin 2016). In contrast, longer-lived south temperate species reduced parental feeding rates in response to increased offspring predation risk to a lesser degree than shorter-lived north temperate species (Ghalambor & Martin 2001; Lloyd et al. 2014). However, parental feeding activity can exacerbate predation risk by attracting attention to the nest (Martin et al. 2000; Muchai & du Pleiss 2005), so reduced activity when predation risk is elevated could indicate decreased parental effort and a strategy to prevent predators from finding their nest (Martin et al. 2000; Muchai & du Pleiss 2005; Martin 2015). Hence, it is difficult to separate the two hypotheses on the basis of feeding rates alone.

Other work has provided some support for the *risk mitigation hypothesis*. Species with higher mean nest predation rates decreased feeding rates to a greater extent than species with lower nest predation rates when exposed to a model nest predator for a short period of time (Ghalambor et al. 2013). Since behavioral traits are responsive to environmental cues in the short term, parents may be able to compensate for reducing care when a predator is present by providing additional care once the predator leaves (Lima & Bednekoff 1998). In contrast, we manipulated perceived predation risk over the course of weeks and measured egg size, clutch mass, incubation attentiveness, and incubation period that are either fixed or expressed over a longer period of time preventing compensation. Thus, responses to predation risk in these traits may be more relevant for future parental fitness than more labile behavioral traits.

Comparative studies across species or populations that differ in likelihood of future reproduction are needed in other taxa to test the generality of our results. Nonetheless, given the importance of offspring predation for fitness across taxa (Eckert 1987; Promislow & Harvey 1990; Martin 1992; Gosselin & Qian 1997; Martin et al. 2017), variation in iteroparity and lifespan may underlie interspecific differences in predator-induced plasticity in parental care traits more broadly.

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References:

Benard, MF. 2004 Predator-induced phenotypic plasticity in organisms with complex life histories. *Annu. Rev. Ecol. Evol. Syst.* ***35***, 651-673.

Clark, CW. 1994 Antipredator behavior and the asset-protection principle. *Behav. Ecol.* ***5*,** 159-170.

Coslovsky, M, Richner, H. 2011 Predation risk affects offspring growth via maternal effects. *Func. Ecol.* ***25***, 878-888.

Creel, S, Christianson, D. 2008 Relationships between direct predation and risk effects. *Trends Ecol. Evol.* ***23***, 194-201.

DuRant, SE, Hopkins, WA, Hawley, DM, Hepp, GR. 2012 Incubation temperature affects multiple measures of immunocompetence in young wood ducks (*Aix sponsa*). **8**, 108-111.

Eckert, GJ. 1987 Estimates of adult and juvenile mortality for labrid fishes at One Tree Reef, Great Barrier Reef. *Mar. Biol.* **95**, 167-171.

Fontaine, JJ, Martin, TE. 2006 Parent birds assess nest predation risk and adjust their reproductive strategies. *Ecol. Lett.* **9**, 428-434.

Gadgil, M, Bossert, WH. 1970 Life historical consequences of natural selection. *Am. Nat.* **104**, 1-24.

Ghalambor, CK, Martin, TE. 2001 Fecundity-survival trade-offs and parental risk-taking in birds. *Science* ***292***, 494-497.

Ghalambor, CK, Peluc, SI, Martin, TE. 2013 Plasticity of parental care under the risk of predation: how much should parents reduce care? *Biol. Lett.* **9**, 20130154.

Giesing, ER, Suski, CD, Warner, RE, Bell, AM. 2011 Female sticklebacks transfer information via eggs: effects of maternal experience with predators on offspring. *Proc. R. Soc. B* **278**, 1753-1759.

Gosselin, LA, Qian, PY. 1997 Juvenile mortality in benthic marine invertebrates. *Mar. Ecol. Prog. Ser.* **146**, 265-282

Hepp, GR, Kennamer, RA. 2012 Warm is better: Incubation temperature influences apparent survival and recruitment of wood ducks (*Aix sponsa*). **10**, e47777. Doi:10.1371/journal.pone.0047777.

Krist, M. 2011 Egg size and offspring quality: a meta-analysis in birds. *Biol. Rev.* **86**, 692-716.

LaManna, JA, Martin, TE. 2016 Costs of fear: behavioural and life-history responses to risk and their demographic consequences vary across species. *Ecol. Lett.* **19**, 403-413.

Law, R. 1979 Optimal life histories under age-specific predation. *Am. Nat.* **114**, 399-417.

Lima, SL, Bednekoff, PA. 1999 Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *Am. Nat.* **6**, 649-659.

Lima, SL, Dill, LM. 1990 Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* ***68***, 619-640.

Lloyd, P, Abadi, F, Altwegg, R, Martin, TE. 2014 South-temperate birds have higher apparent adult survival than tropical birds in Africa. *J. Avian Biol.* **45**, 493-500.

Marshall, DJ, Uller, T. 2007 When is a maternal effect adaptive? *Oikos*, **116**, 1957-1963.

Martin, TE, Boyce, AJ, Fierro-Calderon, K, Mitchell, AE, Armstad, CE, Mouton, JC, Bin Soudi, EE. 2017 Enclosed nests may provide greater thermal than nest predation benefits compared with open nests across latitudes. *Func. Ecol.* **31**, 1231-1240.

Martin, TE, Briskie, JV. 2009 Predation on dependent offspring: a review of the consequences for mean expression and phenotypic plasticity in avian life history traits. *Ann. NY Acad. Sci.* **1168**, 201-217.

Martin, TE, Scott, J, Menge, C. 2000 Nest predation increases with parental activity: separating nest site and parental activity effects. *Proc. R. Soc. B* **267**, 2287-2293.

Michod, RE. 1979 Evolution of life histories in response to age-specific mortality factors. *Am. Nat.* **133**, 531-550.

Monaghan, P, Nager, RG, Houston, DC. 1998 The price of eggs: increased in egg production reduces the offspring rearing capacity of parents. *Proc. R. Soc. B* **265**,1731-1735.

Muchai, M, Plessis, MAD. 2005 Nest predation of grassland bird species increases with parental activity at the nest. *J. Avian Biol.* ***36***, 110-116.

Nager, RG, Monaghan, P, Houston, DC. 2001 The cost of egg production: increased egg production reduces future fitness in gulls. *J. Avian Biol.* **32**, 159-166.

Promislow, DE, Harvey, PH. 1990 Living fast and dying young: A comparative analysis of life-history variation among mammals. *J. Zool.* **220**, 417-437.

Reid, JM, Monaghan, P, Ruxton, GD. 2000 Resource allocation between reproductive phases: the importance of thermal conditions in determining the costs of incubation. *Proc. R. Soc. B* **267**, 37-41.

Sheriff, MJ, Love, OP. 2013 Determining the adaptive potential of maternal stress. *Ecol. Lett.* **16**, 271-280.

Ton, R, Martin, TE. 2017 Proximate effects of temperature versus evolved intrinsic constraints for embryonic development times among temperate and tropical songbirds. *Sci. Rep.* **7**, 895, doi:10.1038/s41598-017-00885-3.

Visser, ME, Lessells, CM. 2001 The costs of egg production and incubation in great tits (*Parus major*). *Proc. R. Soc. B* **268**, 1271-1277.

Tables:

Table 1: Life history characteristics of study species.

Species	English Name	Nest Location	Adult Survival	Nest Predation
Troglodytes aedon	House Wren	Cavity	0.434	0.005
Sialia mexicana	Western Bluebird	Cavity	0.477	0.007
Junco hyemalis	Dark-eyed Junco	Ground	0.570	0.041
Cardellina rubrifrons	Red-faced Warbler	Ground	0.587	0.037

Figure Captions:

Fig. 1: Predictions of the **(A)** *risk mitigation hypothesis* and the **(B)** *reproductive value hypothesis*.

Fig. 2: Standardized effect sizes (standardized regression coefficients ± 1 SE) for **(A)** egg mass, **(B)** clutch mass, **(C)** incubation attentiveness, and **(D)** incubation period length. Cavity nesting species with low adult survival and low nest predation rates are depicted in yellow. Ground nesting species with high adult survival and high nest predation rates are depicted in blue.

Figures:

Fig. 1:

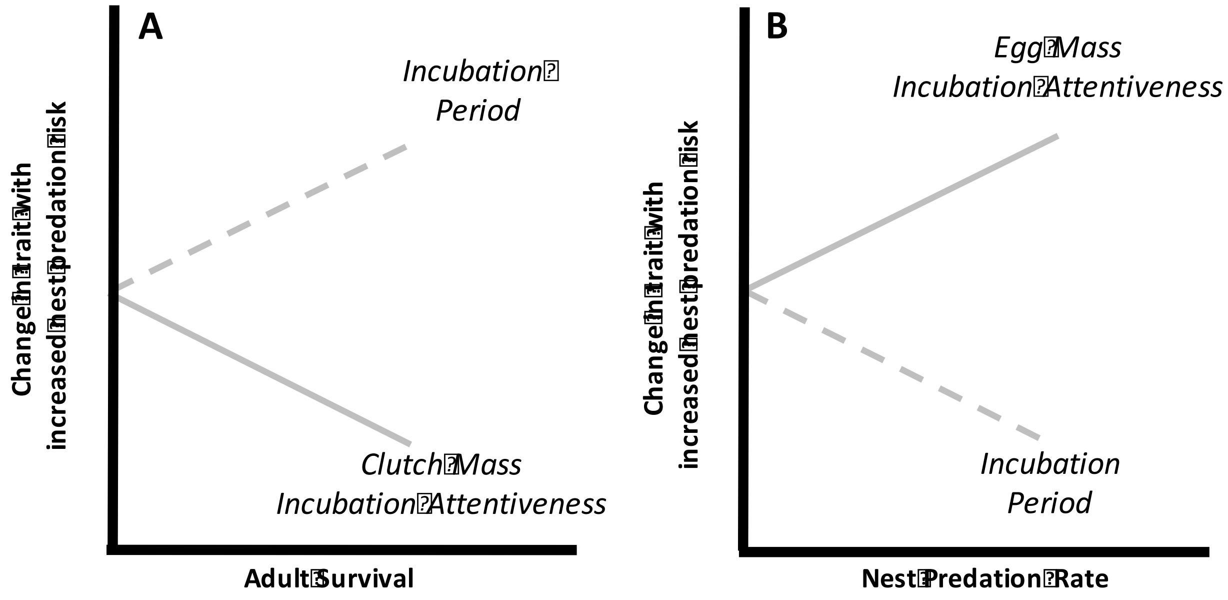
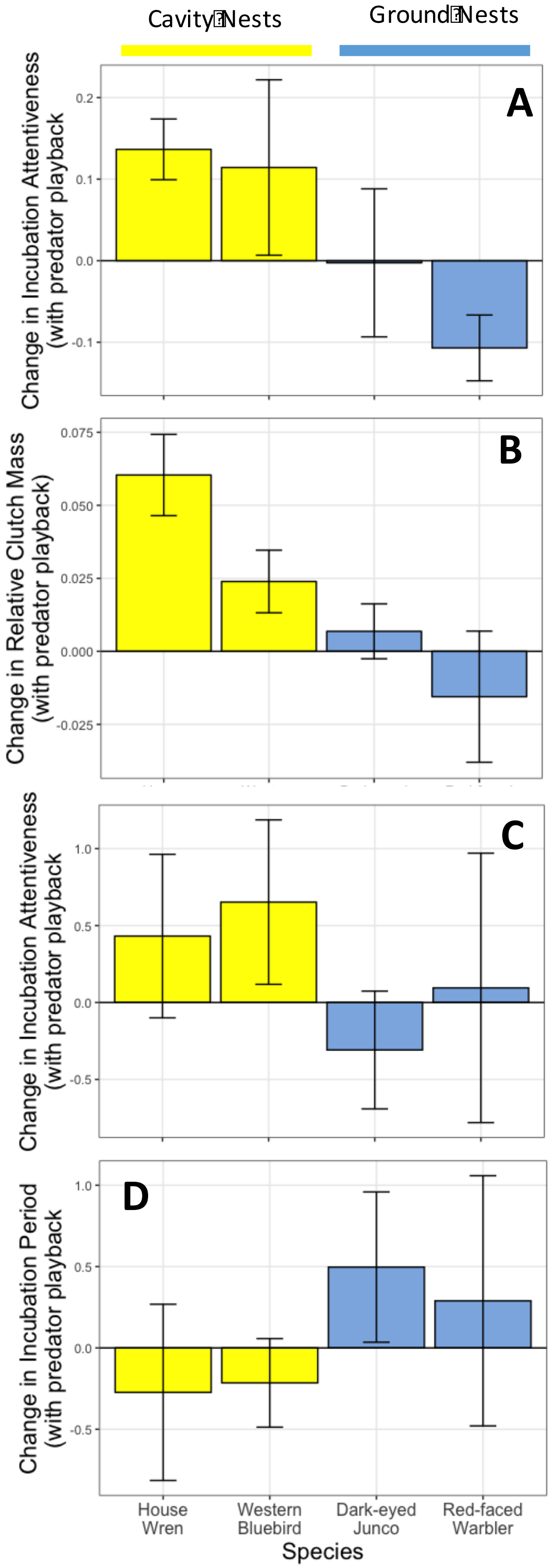


Fig. 2:


Cavity Nests
Ground Nests
A
Change in Incubation Attentiveness
(with predator playback
0.2
0.1
0.0
-0.1
B
Change in Relative Clutch Mass
(with predator playback)
0.075
0.050
0.025
0.000
-0.025
C
Change in Incubation Attentiveness
(with predator playback
1.0
0.5
0.0
-0.5
D
Change in Incubation Period
(with predator playback
1.0
0.5
0.0
-0.5
House Wren
Western Bluebird
Dark-eyed Junco
Red-faced Warbler
Species

CHAPTER 3: FITNESS CONSEQUENCES OF INTERSPECIFIC NESTING ASSOCIATIONS AMONG CAVITY NESTING BIRDS

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***Abstract**:*

Interspecific aggregations of prey may provide benefits by mitigating predation risk, but they can also create costs if they increase competition for resources or are more easily detectable by predators. Variation in predation risk and resource availability may influence the occurrence and fitness effects of aggregating in nature. Yet, tests of such possibilities are lacking. Cavity nesting birds provide an interesting test case. They compete aggressively for resources and experience low nest predation rates, which might predict dispersion, but we found they commonly aggregate by sharing nest trees across 19 years of study. Tree sharing was more common when aspen were more abundant and somewhat more common in years with higher nest predation risk. Nest success was higher in shared trees when nest predation risk was higher than average. Ultimately, the costs and benefits of aggregating (nest tree sharing) varied across years and we outline hypotheses for future studies.

Introduction:

Aggregation of species can incur costs and benefits from predation and competition that influence fitness, and shape the extent of aggregating in nature. Less aggregation and greater dispersion should be favored when prey aggressively compete for limited resources (Orians and Wilson 1964; MacArthur and Levins 1967). Similarly, prey may avoid predators by becoming more dispersed and less conspicuous (Inmam and Krebs 1987; Martin 1988, 1993a, 1996; Martin et al. 2000; Varela et al. 2007). In contrast, among species that have mutual predators, interspecific aggregations may prove beneficial through risk dilution, earlier detection of predators and more effective defense (Hamilton 1971; Morse 1977; Quinn and Ueta 2008; Krams et al. 2010). In either of these cases, the cost and benefits of interspecific aggregations may be dependent on the levels of both predation risk and the intensity of competitive interactions, and each can change over time (Agrawal et al. 2007; Chamberlain et al. 2014). Yet the influence of variation in both predation risk and competition on spatial associations among species and their fitness consequences is poorly understood.

Species with high levels of resource overlap and heterospecific aggression are generally unlikely to aggregate, but may be more likely to do so under certain environmental conditions (Orians and Wilson 1964; MacArthur and Levins 1967; Peiman and Robnson 2010). For example, while aggressive interactions over access to shared resources can lead to increased dispersion when one species excludes another from the area around a resource, aggression is thought to be less important when resources are abundant (Brown 1975; Peiman and Robinson 2010). Thus, when resources are abundant, aggregating may become more common, even among species with high levels of resource overlap. Furthermore, if aggregating species gain benefits from reduced predation risk, the benefits of aggregating may compensate for any costs due to aggressive interactions especially when resources are abundant or predation risk is elevated. Still, for species that experience low predation rates on average, benefits of further reductions in predation risk may be relatively unimportant and costs of aggression should be predominant. Thus, species with low predation rates that aggressively compete for defendable resources should generally avoid aggregating unless predation risk or resource availability are particularly high.

Cavity nesting birds provide an interesting system to test these ideas. They have low nest predation rates (Nice 1957; Martin 1995; Fontaine et al. 2007) and often compete for limited nest sites, aggressively excluding other cavity nesting species from the areas around their nests to prevent nest takeover attempts (Short 1979; Nilsson 1984; Ingold 1994; Newton 1994; Duckworth 2006). In addition, many cavity nesting species also overlap in foraging sites and food resources (e.g., Bull et al. 1986) which could exacerbate aggressive interactions. These conditions predict dispersion of species, but different cavity nesting species have been observed nesting in the same tree (Hoyt 1948; Reller 1971; McClelland 1977; Belson 2000). However, the extent of nest tree sharing is not well described, and costs and benefits of sharing are unstudied, especially with respect to temporal variation in nest predation risk and resource availability.

Variation in nest predation risk and nest tree availability could influence the incidence and fitness effect of tree sharing in several ways (fig. 1). First, limited availability of nest trees may force cavity nesting birds to share trees because there are no other suitable sites. If nest site limitation forces sharing, then sharing should be more common when nest trees are more limited (fig. 1A). In contrast, aggression among species at nests may be more severe when either nest site or food resources are limited (Peiman and Robinson 2010), causing sharing to be less common (fig. 1B). In either case, greater aggression among cavity nesting species with greater resource overlap in nest site or food resources may limit which species commonly share nest trees (fig. 1C; Brown and Wilson 1956; MacArthur 1972; Hespenheide 1973; Short 1979; Nilsson 1984). Sharing nest trees may also have benefits when nest predation risk is elevated because multiple pairs of adults can better deter potential predators and increase the likelihood of successfully fledging young (fig. 1D-E; reviewed in Quinn and Ueta 2008). This benefit may particularly strong for small species which may be less likely to be able to deter potential predators than larger species (fig. 1F). On the other hand, higher levels of parental activity of multiple pairs might attract predators (Skutch 1949; Martin et al. 2000) and increase costs of sharing when nest predation risk is high (fig. 1G-H). In contrast, when the risk of nest predation is low, energetic costs from aggressive encounters may outweigh any potential gains in nest success. In this case, breeding adults may more commonly nest alone on trees and adopt other strategies to reduce predation risk. Resolution of these alternatives requires examination of the incidence and consequences of sharing nest trees under different levels of resource availability and nest predation risk.

We used 19 years of nesting data to test these *a priori* hypotheses and consider additional alternatives in the discussion. First, we provide a general description of the incidence and habitat characteristics associated with nest tree sharing in a community of cavity nesting birds. Specifically, we assess whether species were more likely to share trees with other species that have less resource overlap. Second, we examine whether variation in nest predation risk and aspen abundance across years explains variation in the prevalence of shared nest trees. Because aspen are preferred nesting trees (Li and Martin 1991; Martin et al. 2004; Martin 2014), years with high aspen abundance may reflect high nest tree availability although greater aspen abundance could also correlate with higher food availability. Finally, we examine how sharing a nest tree influences reproductive success and whether reproductive consequences change with variation in nest predation risk across years. Ultimately, the well documented interference competition for nest sites and low predation rates among cavity nesters raises questions about why nest tree sharing occurs. Understanding how predation risk and interference competition shape nest tree sharing can provide new insight into the role of environmental variation for other interspecific associations and their fitness consequences.

Materials and Methods:

Study areas and species:

We studied cavity nesting birds at a mid-elevation (2350 m) mixed forest field site in Arizona, USA (34_o N) from 1993 to 2011. This site provided an excellent system to address our questions because both nest predation risk and the abundance of the preferred nest tree species (Quaking Aspen – *Populus tremuloides*) varied across years (Li and Martin 1991; Martin 2014).

We found and monitored cavity nests for 5 common woodpeckers (Downy Woodpecker (*Picoides pubescens*), Hairy Woodpecker (*Picoides villosus*), Williamson's Sapsucker (*Sphyrapicus thyroideus*), Red-naped Sapsucker (*Sphyrapicus nuchalis*), and Northern Flicker (*Colaptes auratus*)) and 5 common passerines (House Wren (*Troglodytes aedon*), Red-breasted Nuthatch (*Sitta canadensis*), White-breasted Nuthatch (*Sitta carolinensis*), Western Bluebird (*Sialia mexicana*), and Mountain Chickadee (*Parus gambeli*)). All woodpeckers and one species of passerine (Red-breasted Nuthatch) are capable of excavating new cavities. However, both excavating and non-excavating species make regular use of previously existing cavities (Martin 1993b).

Data collection:

Nests were found using parental behavior and systematic search, and monitored every 2-4 days (Martin and Guepel 1993). Nests were designated as in a shared tree when two nests were simultaneously active in the same tree. Nests were considered successful when at least one nestling was confirmed to have fledged or the nest became inactive within two days of the end of the average nestling period for that species (Martin and Geupel 1993).

After nests became inactive, various characteristics of the cavity, nest tree, and nest patch were recorded. We recorded the height, visibility (crypsis), and type of cavity (old, freshly excavated, natural) for each nest. The status (live vs. dead) and the number of additional cavities on each tree seen from the ground were also recorded. At the patch level, the number and species of trees were counted within 11 m of a nest tree. Each year starting in 1995, we also estimated the abundance of most cavity nesting species across our site using the plot mapping technique (Christman 1984; Martin 2014) and the abundance of aspen by following the fates of permanently marked trees (Martin 2007, 2014). See the supplementary material for more detailed methods.

Statistical analyses:

Occurrence of shared nest trees: We tested whether resource overlap explained which species were more likely to share nest trees by examining differences in mass and phylogenetic distances. Because small entrance holes can exclude potential nest predators and larger nest site competitors, species are thought to prefer cavities with the smallest possible entrances (Short 1979; Nilsson 1984; Martin et al. 2004). Thus, we used differences in body mass between species to indicate overlap in nest site resources. We used phylogenetic distance between species as a more general proxy for ecological differences between species, including food and nest site resource overlap. We include matrices containing these variables in two separate partial mantel tests, which controlled for differences in preferences for live or dead aspen (Martin 2014). We used species masses from our site published elsewhere (Li and Martin 1991). Phylogenetic distances were obtained from a majority rules consensus tree constructed from 1000 trees using program Mesquite (Maddison and Maddison 2011). Phylogenetic trees were downloaded from www.birdtree.org (Jetz et al 2012) using the Hackett et al. (2008) backbone.

Resource overlap and interference competition might also influence the vertical distance between nests on shared trees. To test this idea, we used a linear mixed model with the distance between each nest as the response variable, the difference in mass and the number of cavities in the tree as explanatory variables and year as a random effect. We limited this analysis to trees with at least one unoccupied cavity.

To characterize any differences in the habitat around shared nest trees, we used a logistic mixed model with sharing as the response variable. We included the abundance of live aspen, dead aspen, live conifers, and other live deciduous tree species within 11m of the nest tree as well as the total number of cavities in the nest tree, nest height, nest crypsis, the status of the nest tree (dead vs. live), and the type of cavity as explanatory variables. Year and species were included as random effects.

Proportion of shared nest trees over time: We used linear models to test for the effect of aspen abundance and nest predation risk on the proportion of nests shared each year. We included the number of aspen still standing as an explanatory variable, and controlled for the total density of cavity nesters and the density of woodpeckers in the previous year because this may affect cavity availability and quality (Norris and Martin 2010). Finally, we included average annual nest predation rates to test the role of predation risk. We estimated nest predation rates using the logistic exposure method including year as a fixed effect and species as a random effect (Shaffer 2004).

Reproductive success: We used the logistic exposure method (Schaffer 2004) to examine whether nest tree sharing influenced reproductive success. Because nest site characteristics can strongly influence reproductive success, we first ran a model without tree sharing to find the best predictors of nest success to include in subsequent models. We chose to use an information-theoretic approach based on Akaike's Information Criterion (AIC) because traditional hypothesis-testing based on p-values in logit models containing interaction terms can be problematic (Berry et al. 2010). We created a set of candidate models based on the hypotheses that there is an effect of nest tree sharing on nest success and this effect may vary with mean annual nest predation risk, body mass, or both. Random effects for year and species were included in all models.

Additional methodical details are included in the supplemental material. Data are deposited to Dryad (Mouton and Martin 2018; doi:10.5061/dryad.b71g0gr).

Results:

Occurrence of shared nest trees: We found 5966 nests overall of which 841 were located in shared nest trees. The proportion of nests occurring in shared nest trees varied between 0-30.9% across years (mean = 15.1%). Most shared nest trees included exactly two nests (85%) although there were trees with larger numbers of nests (15%). 50.9% of unshared nest trees and 68.8% of shared nest trees had unoccupied visible cavities. No cases of intraspecific sharing were observed. The number of nests shared by all pairs of species increased with both the mass ratio (greater ratio reflects greater difference) between species (Partial Mantel Test: $r = 0.364$, $p = 0.046$; fig. 2A, B; fig. A1) and their phylogenetic relatedness (Partial Mantel Test: $r = 0.358$, $p = 0.001$). Nests in shared trees were closer in vertical distance on the trunk of the tree with greater differences in masses between species (mass ratio: $b = -0.032$, $t = -2.551$, $p = 0.011$; number of cavities in tree: $b = 0.014$, $t = 1.755$, $p = 0.085$, $n = 212$; fig. 2C).

Nests in shared trees were less cryptic ($b = -0.271$, $z = -2.546$, $p = 0.010$; table A1), less likely in natural cavities than either old ($b = 1.673$, $z = 5.036$, $p <0.001$; table A1) or freshly excavated ($b = 1.066$, $z = 2.997$, p 0.002; table A1) cavities, and were marginally higher than solitary nests ($b = 0.207$, $z = 1.833$, $p = 0.066$; table A1). Shared nest trees also had more observed cavities ($b = 0.467$, $z = 7.931$, $p < 0.001$; table A1) and were marginally more likely to be in patches with greater density of aspen snags ($b = 0.034$, $z = 1.929$, $p = 0.053$; table A1) than unshared nest trees. Similar patterns existed when considering only non-excavating species, but only the number of cavities in a tree explained tree sharing for excavating species ($b = 0.406$, $z = 4.839$, $p < 0.001$; table A1).

Proportion of shared nests over tim:e The proportion of nests in shared trees increased with the number of standing aspen in that year ($b = 0.667$, $t = 4.371$, $p = 0.001$; table A2; fig. 3A), decreased with woodpecker density in the previous year ($b = -0.303$, $t = -2.395$, $p = 0.035$; table A2; fig. 3B), and marginally increased with annual nest predation rates ($b = 0.093$, $t = 2.118$, $p = 0.057$; table A2; fig. 3C).

Reproductive success: Overall, 79.7% and 90.5% of solitary and shared nests fledged young, respectively. Among the nest site characteristics that predicted if a nest tree would be shared, only cavity type explained the probability that a nest succeeded (nest height: $p = 0.893$; number of observed cavities: $p = 0.142$; nest crypsis: $p = 0.924$; number of dead aspen within 11m: $p=0.978$; old vs. natural cavities: $p = 0.015$; fresh vs. natural cavities: $p = 0.129$). We found strong support for larger increases in nest success in shared trees in years with above average nest predation risk (AIC weight: 0.995; fig. 4; table A3). Models suggesting greater benefits of tree sharing in species with smaller body mass also had some support (AIC weight: 0.626; fig. 4; table A3).

Discussion:

Theory predicts higher dispersion and less aggregation among species with high resource overlap and low average predation rates. Mixed-species aggregations may be particularly rare and costly when species show high levels of heterospecific aggression and exclude each other from around resources. Cavity nesting birds are generally thought to fit these criteria and yet, here, we show that they regularly nest together on the same tree. These results raise the question: why does nest tree sharing occur? That the extent of nest tree sharing fluctuated over time with variation in resource levels and nest predation risk points to several possible explanations.

Benefits due to reducing predation risk may promote nest tree sharing. In theory, nesting in close proximity to other birds could provide earlier detection and more effective deterrence of approaching predators. We found that nests in shared trees had higher probability of fledging young than solitary nests in years with higher than average levels of nest predation risk (fig. 4; table A3). Furthermore, we found that nest tree sharing was somewhat more common in years when nest predation risk was high (fig. 3; table A2). Together, these results point to the possibility that cavity nesting birds may plastically respond to cues about nest predation risk early in the breeding season (e.g. Hua et al. 2013) by sharing nest trees to mitigate that risk. Alternatively, these patterns may reflect higher breeding densities in relatively safer areas in high risk years which results in greater overlap in habitat selection, increased sharing and higher nest success. Furthermore, benefits in nest success rates might be offset by costs in the quality or quantity of young produced, or parental condition, from increased aggressive interactions with neighbors to thereby explain why sharing is less common than solitary nesting. Thus, ultimately, studies examining spatial patterns of predation risk and experiments using more comprehensive metrics of reproductive success and parental condition are needed to fully understand the fitness consequences of nest-tree sharing.

Several pieces of evidence suggest a role for interference competition in shaping the extent of tree sharing among species. Shared nest trees were more common in years when aspen were more abundant (fig. 3; table A2) and aggressive interactions over resources, either nest sites or food, should be less intense (Peiman and Robinson 2010). Thus, it seems shared nest trees were most prevalent in situations where preferred nest trees were most abundant, conflicting with the idea that limited nest trees may force nest tree sharing due to lack of alternative options. Instead, interference competition may be more severe when nest site or food resources are scarce, making it especially costly to share nest trees under those conditions (Peiman and Robinson 2010). Nonetheless, the degree to which aspen abundance reflects nest site or food availability is unclear and should be addressed in future studies.

Given that aggressive interactions should be more intense among species with greater nest site or food overlap (Macarthur and Levins 1967; Peiman and Robinson 2010), interference competition may also limit which species share nest trees. Indeed, shared nest trees were less common among species with similar body sizes and those that were more closely related phylogenetically. However, increased nest tree sharing among dissimilar species could also arise because smaller, more vulnerable passerines prefer to nest with larger species that provide the best protection from nest predators. Indeed, we did find some support for the idea that smaller species benefited more from tree sharing than larger species although the effect seems to be fairly negligible especially in years with low predation risk (fig. 4; table A3). However, the result that species pairs with more similar body sizes tended to nest farther apart on shared nest trees emphasizes a role for interference in shaping which species will nest together because higher levels of aggression between more similar species may favor increased dispersion even on the same tree (fig. 2C; Duckworth 2006). Thus, our result are consistent with the idea that interference competition over cavities or food resources limits tree sharing among cavity nesters. Nonetheless, direct measures of aggressive behavior at various spatial scales are lacking and studies assaying heterospecific aggression at different levels of food and nest site availability and at various spatial scales are needed.

Variation in cavity quality may also play an important role in the extent of tree sharing. Woodpeckers are thought to excavate high quality cavities that other species use but they deteriorate over time such that more recently excavated cavities provide the greatest benefits (Aitken et al. 2002; Martin et al. 2004). When they are available, recently excavated woodpecker cavities may provide an alternate way to mitigate nest predation risk without incurring costs due to aggressive interactions with neighbors. Indeed, we found that in years following relatively higher densities of woodpeckers, when more high quality cavities were likely available, fewer nests were in shared nest trees. However, freshly excavated cavities did not have higher nest success than old or natural cavities in our system (see results). Still, we could not distinguish the ages of cavities excavated in previous years and, so, the tradeoffs between cavity quality and nest-tree sharing remain unclear.

Overall, we show that despite the well documented aggression among cavity nesting birds for nest sites, sharing nest trees can be common under certain environmental circumstances and that nest success seems to be higher for nests in shared versus unshared trees. We discuss several possible explanations for these phenomena, but ultimately experiments are needed to tease them apart. Our results highlight the need to consider how environmental variation may influence mixed species associations in other taxa. Indeed, examination of environmental variation that can shift the balance between costs and benefits of aggregating may help both identify other unlikely associations among species and suggest the mechanisms that underlie them.

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Supplementary Materials:

Data Collection:

Nests were considered successful when at least one nestling was confirmed to have fledged or the nest became inactive within two days of the end of the average nestling period for that species (Martin and Geupel 1993). We assumed all nest failures after eggs were laid to be due to nest predation unless there was any evidence to the contrary. For example, in several cases adults were not seen in the territory again or remains were found suggesting predation of the adults explained the failure (11 nests) or inclement weather was implicated (3 nests). We removed these nests from data prior to analysis of nest success rates. A few rare or sporadically distributed cavity nesting species were present at our field site and were present in shared nest trees. These species were considered when determining the overall prevalence of tree sharing, but all subsequent analyses were limited to the ten common species which had adequate information to determine nest fate.

Nest height was measured using a clinometer. Nest crypsis was scored on a scale of 0 – 4 (0 = no concealment, 4 = extremely cryptic) based on any vegetation, peeling bark, dark or light patches, branches or knots that camouflaged or otherwise obscured visibility of the nest. Cavity type determined by examining the shape of a cavity's entrance to determine if it had originally been excavated by a bird (circular) or was a natural cavity formed by other means (irregular). Excavated cavities were further scored as freshly excavated or as old based on the presence of brighter, less weathered wood around the entrance or fresh wood chips at the base of the tree Martin 1993b). This allowed us to distinguish cavities excavated in the current season from older cavities, but did not allow us to differentiate older cavities by age. A small number of nests that were located in nest boxes were removed from data prior to statistical analyses. The status of the nest tree was scored as dead or alive based on the presence and appearance of the leaves (Martin 2014). Trees which had dead portions were scored as being still alive. We followed published methods for measuring vegetation characteristics in the patch around nest trees (BBIRD Field Protocols; Martin et al. 1997). Briefly, we counted and identified the species of all trees within 11.3 meters of the nest with a diameter at breast height (DBH) greater than 8 cm for live trees and 23 cm for dead trees.

Statistical Analyses:

Reproductive success: We used the logistic exposure method (Schaffer 2004) to test whether nest tree sharing influenced reproductive success. Because nest site characteristics can strongly influence reproductive success, we identified nest site covariates using a model that included the number of observed cavities in the nest tree, status of the nest tree (live or dead), cavity type (natural, freshly excavated, or excavated in a previous year), nest crypsis, nest height in meters, and the number of aspen, conifer, and other deciduous trees within 11m in a full model with random effects for year and species. We mean-centered all 11m tree counts and nest height variables. We included all significant predictors from this model (tree heath, nest height, live aspen within 11m) as covariates in all subsequent models. We used AIC to compare a set of models including nest site covariates with and without a term specifying if a nest was in a shared tree and also models with interactions between tree sharing, mean annual nest predation rates, and/or taxonomic order (Piciformes: woodpecker or Passeriformes: songbird). We only knew the fate and had measurements for all nest site covariates for a subset of nests we found. Ultimately, nest success analyses included 2264 nests (404 in shared trees and 1860 in solitary trees) with 1850 successfully fledging young (366 in shared trees and 1484 in solitary trees).

All analyses were performed in R (R Core Development Team 2017) using the lme4 (Bates et al. 2015) and vegan (Oksanen et al. 2016) packages.

Table A1: Habitat characteristics of shared nest trees for (a) all species, (b) excavating species, and (c) non-excavating species. We show coefficients and standard errors (*B* (*se*)), *z*-values, and significance from a logistic mixed model.

(a) Habitat characteristics of shared nest trees (all species)

Fixed effect	*B (se)*	*z*	*P-value*
Nest height	0.218 (0.112)	1.945	0.051
Number of cavities	0.467 (0.058)	7.931	<0.001
Nest Crypsis	-0.259 (0.105)	-2.470	0.013
Dead tree (vs. Live)	-0.210 (0.146)	-1.442	0.149
Old cavity (vs. Natural cavity)	1.673 (0.332)	5.036	<0.001
Fresh cavity (vs. Natural cavity)	1.066 (0.355)	2.997	0.002
Dead aspen within 11m	0.034 (0.017)	1.929	0.053
Conifer trees within 11m	-0.001 (0.086)	-0.006	0.995
Deciduous trees within 11m	-0.086 (0.076)	-1.138	0.255
Live aspen within 11m	-0.023 (0.036)	-0.637	0.524

Random effect	*Variance*	*Std. Dev.*
Year	1.392	1.180
Species	0.2302	0.479

(b) Habitat characteristics of shared nest trees (excavators only)

Fixed effect	*B (se)*	*z*	*P-value*
Nest height	0.274 (0.180)	1.522	0.127
Number of cavities	0.406 (0.084)	4.839	<0.001
Nest Crypsis	-0.223 (0.147)	-1.514	0.130
Dead tree (vs. Live)	0.278 (0.222)	1.254	0.209
Old cavity (vs. Natural cavity)	0.137 (0.513)	0.268	0.788
Fresh cavity (vs. Natural cavity)	-0.599 (0.506)	-1.184	0.236
Dead aspen within 11m	0.012 (0.022)	0.529	0.596
Conifer trees within 11m	0.001 (0.119)	0.011	0.990
Deciduous trees within 11m	-0.133 (0.111)	-1.195	0.231
Live aspen within 11m	-0.033 (0.052)	-0.629	0.529

Random effect	*Variance*	*Std. Dev.*
Year	1.641	1.281
Species	0.295	0.543

(c) Habitat characteristics of shared nest trees (Non-excavators only)

Variable	*B (se)*	*z*	*P-value*
Nest height	0.202 (0.150)	1.345	0.178
Number of cavities	0.505 (0.083)	6.027	<0.001
Nest Crypsis	-0.355 (0.155)	-2.288	0.022
Dead tree (vs. Live)	-0.646 (0.206)	-3.136	0.001
Old cavity (vs. Natural cavity)	2.511 (0.480)	5.231	<0.001
Fresh cavity (vs. Natural cavity)	2.237 (0.566)	3.951	<0.001

Dead aspen within 11m	0.087 (0.032)	2.714	0.006
Conifer trees within 11m	-0.023 (0.129)	-0.184	0.854
Deciduous trees within 11m	0.004 (0.108)	0.043	0.966
Live aspen within 11m	-0.009 (0.052)	-0.174	0.862

Random effect	*Variance*	*Std. Dev.*
Year	1.091	1.045
Species	0.334	0.578

Table A2: Frequency of nests occurring on shared nest trees in relation to nest predation risk, aspen availability, woodpecker density in previous years, and the density of cavity nesters in the current year. We show coefficients and standard errors (*B* (*se*)), *t*-values, and significance from linear models.

Proportion of nests in shared trees across years (Adj. R_2=0.751)

Variable	*B (se)*	*t*	*df*	*P-value*
Log Nest Predation Risk	0.093 (0.044)	2.118	1	0.057
Log Aspen Count	0.667 (0.152)	4.371	1	0.001
Log Previous Year Woodpecker Density	-0.303 (0.126)	-2.395	1	0.035
Log Cavity Nester Density	0.098 (0.181)	0.546	1	0.596
Error			11	

Table A3: AIC table for models testing whether sharing a nest tree influences nest success. All models include habitat covariates and random effects for both year and species. We report the number of parameters (*K*), the log likelihood, AIC values, differences in AIC values (Δ_i), and Akaike weights (w_i) for all models.

Interactions Terms in Model	*K*	*Log Likelihood*	*AIC*	Δ_i	w_i
Nest Predation Risk + Body Mass	9	-761.277	1544.6	0.00	0.491
Nest Predation Risk	7	-763.559	1545.1	0.56	0.371
Nest Predation Risk * Body Mass	11	-760.583	1547.2	2.61	0.133
Body Mass	7	-768.624	1555.2	10.69	0.002
No Interaction	5	-770.831	1555.7	11.11	0.002
No Shared Tree term	4	-773.032	1558.1	13.15	0.001

References:

Agrawal, A. A., D. D. Ackerly, F. Adler, A. E. Arnold, C. Cáceres, D. F. Doak, E. Post, P. J. Hudson, J. Maron, K. A. Mooney, M. Power, D. Schemske, J. Stachowicz, S. Strauss, M. G. Turner, and E. Werner. 2007. Filling key gaps in population and community ecology. Frontiers in Ecology and the Environment 5:145-152.

Aitken, K. E. H., K. L. Wiebe, and K. Martin. 2002. Nest-site reuse patterns for a cavity-nesting bird community in interior British Columbia. The Auk 119: 391-402.

Belson, M. S. 2000. Simultaneous use of a snag by three breeding birds in central Florida. Florida Field Naturalist 28:115-117.

Berry, W. D., J. H. R. DeMeritt, and J. Esarey. 2010. Testing for interaction in binary logit and probit models: is a product term essential? American Journal of Political Science 54:248-266.

Brown, J. H. 1975. Geographical ecology of desert rodents. Pages 315-341 *in* M. L. Cody and J. M. Diamond ed. Ecology and Evolution of Communities. Harvard University Press, Cambridge, MA.

Brown, W. L. and E. O. Wilson. 1956. Character displacement. Systematic Zoology 5:49-64.

Bull, E. L., S. R. Peterson, and J. W. Thomas. 1986. Resource partitioning among woodpeckers in northeastern Oregon (Vol. 444). US Dept. of Agriculture, Forest Service, Pacific Northwest Research Station.

Chamberlain S. A., J. L. Bronstein, and J. A. Rudgers. 2014. How context dependent are species interactions? Ecology Letters doi: 10.1111/ele.12279.

Christman, S. P. 1984. Plot mapping: estimating densities of breeding bird territories by combining spot mapping and transect techniques. Condor 86:237-241.

Duckworth, R. A. 2006. Behavioral correlations across breeding contexts provide a mechanism for a cost of aggression. Behavioral Ecology doi:10.1093/beheco/arl035.

Fontaine, J. J., M. Martel, H. M. Markland, A. M. Niklison, K. L. Decker and T. E. Martin. 2007. Oikos 116:1887-1894.

Hackett, S. J., R. T. Kimball, S. Reddy, R. C. K. Bowie, E. L. Braun, M. J. Braun, et al. 2008. A phylogenomic study of birds reveals their evolutionary history. Science 320:1763-1768.

Hamilton, W. D. 1971. Geometry for the selfish herd. Journal of Theoretical Ecology 31:295-311.

Hespenheide, H. A. 1973. Ecological inferences from morphological data. Annual Review of Ecology and Systematics 4:213-229.

Hoyt, J. S. Y. 1948. Observations on nesting associates. The Auk 65:188-196.

Hua F., R. J. Fletcher Jr., K. E. Sieving, and R. M. Dorazio. 2013. Too risky to settle: avian community structure changes in response to perceived predation risk on adults and offspring. Proceedings of the Royal Society B 280: 20130762.

Inman, A. J., and J. Krebs. 1987. Predation and group living. Trend in Ecology and Evolution 2:31-32.

Ingold, D. J. 1994. Influence of nest-site competition between Euroean Starlings and Woodpeckers.
Wilson Bulletin 106:227-241.

Jetz, W., G. H. Thomas, J. B. Joy, K. Hartmann, and A. O. Mooers. 2012. The global diversity of birds in space and time. Nature 491:444-448.

Krams, I., A. Berzins, T. Krama, D. Wheatcroft, K. Igaune, and M. J. Rantala. 2010. The increased risk of predation enhances cooperation. Proceedings of the Royal Society B 277:513-518.

Li, P. and T. E. Martin. 1991. Nest-site selection and nesting success of cavity-nesting birds in high elevation forest drainages. The Auk108:405-418.

MacArthur, R. H. 1972. Geographical ecology. Princeton University Press, New Jersey.

MacArthur, R. H. and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. The American Naturalist 101:377-385.

Maddison, W. P., and D. R. Maddison. 2011. Mesquite: A modular system for evolutionary analysis. Version 2.75. http://mesquiteproject.org.

Martin, K., K. E. H. Aitken, and K. L. Wiebe. 2004. Nest sites and nest webs for cavity-nesting communities in interior British Columbia, Canada: nest characteristics and niche partitioning. The Condor 106: 5-19.

Martin, T. E. 1988. On the advantage of being different: Nest predation and the coexistence of bird species. Proceedings of the National Academy of Science 85: 2196-2199.

Martin, T. E. 1993a. Nest predation and nest sites: New perspectives on old patterns. BioScience 43: 523-532.

Martin, T. E. 1993b. Evolutionary determinants of clutch size in cavity-nesting birds: nest predation or limited breeding opportunities? American Naturalist 142: 937-946.

Martin, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. Ecological Monographs 65: 101-127.

Martin, T. E. 1996. Fitness costs of resource overlap among coexisting bird species. Nature 380: 338-340.

Martin, T. E. 2007. Climate correlates of 20 years of trophic changes in a high-elevation riparian system. Ecology 88:367-380.

Martin, T. E. 2014. Consequences of habitat change and resource selection specialization for population limitation in cavity-nesting birds. Journal of Applied Ecology 52:475-485.

Martin, T. E., J. Scott, and C. Menge. 2000. Nest predation increases with parental activity: separating nest site and parental activity effects. Proceedings of the Royal Society London B 267:2287-2293.

Martin, T. E. and G. R. Guepel. 1993. Nest-monitoring plots: methods for locating nest and monitoring success. Journal of Field Ornithology 64:507-519.

McClelland, B. R. 1977. Relationships between hole-nesting birds, forest snags, and decay in Western larch-douglas-fir forests of the Northern Rocky Mountains (PhD). University of Montana.

Morse, D. H. 1977. Feeding behavior and predator avoidance in heterospecific groups. Bioscience 27:332-339.

Newton, I. 1994. The role of nest sites in limiting the numbers of hole-nesting birds: a review. Biological Conservation 70:265-276.

Nice, M. M. 1957. Nesting success in altricial birds. The Auk 74:305-321.

Nilsson, S. G. 1984. The evolution of nest-site selection among hole-nesting birds: the importance of nest predation and competition. Ornis Scandinavica 15:167-175.

Norris, A. R. and K. Martin. 2010. The perils of plasticity: dual resource pulses increase facilitation but destabilize populations of small bodied cavity nesters. Oikos 119:1126-1135.

Orians, G. H. and M. F. Wilson. 1964. Interspecific territories of birds. Ecology 45:736-745.

Peiman, K. S. and B. W. Robinson. 2010. Ecology and evolution of resource-related heterospecific aggression. The Quarterly Review of Biology 85: 133-158.

Quinn, J. L. and M. Ueta. 2008. Protective nesting associations in birds. Ibis 150:146-167.

Reller, A. W. 1971. Aspects of behavioral ecology of red-headed and red-bellied woodpeckers. The American Midland Naturalist 88:270-290.

Shaffer, T. L. 2004. A unified approach to analyzing nest success. The Auk 121:525-540.

Short, L. L. 1979. Burdens of the picid hole-excavating habit. The Wilson Bulletin 91:16-28.

Skutch, A. F. 1949. Do tropical birds rear as many young as they can nourish? Ibis 91:430-458.

Varela, S. A. M., É. Danchin, and R. H. Wagner. 2007. Does predation select for or against avian coloniality? A comparative approach. Journal of Evolutionary Biology 20:1490-1503.

References from the Appendix:

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effect models using lme4. Journal of Statistical Software 67:1-48.

Martin, T.E., C.R. Paine, C.J. Conway, W.M. Hochachka, P. Allen, and W. Jenkins. 1997. BBIRD Field Protocol. Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, Montana, USA.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, et al. 2016. vegan: Community Ecology Package. R package version 2.3-3. http://CRAN.R-project.org/package=vegan.

R Core Development Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Figure Captions:

Figure 1. Hypotheses explaining how resource availability and nest predation risk could influence the occurrence and reproductive success of nest tree sharing. (a) If sharing is a result of nest tree limitation, then the frequency of nest tree sharing should decrease when nest trees are most abundant. In contrast, if heterospecific aggression limits nest tree sharing, then (b) the frequency of nest tree sharing should increase when nest trees are most abundant and (c) species with greater resource overlap should share trees less often because they should exhibit higher levels of aggression towards one another. Variation in nest predation risk could also influence nest tree sharing. If sharing nest trees yields increased nest success due to better detection or deterrence of predators, (d) shared nest trees should be more common and (e) have greater benefits in years with high nest predation risk. Furthermore, if predation benefits of tree sharing are due to better deterrence of predators, (f) smaller species may gain more benefits from sharing nest trees. In contrast, if shared nest trees are more conspicuous to predators, (g) tree sharing may be less common and (h) experience greater costs in years with high nest predation risk.

Figure 2**.** Mass differences between species explained the frequency of sharing between a given species pair. For example, (a) relatively small birds such as the Red-breasted Nuthatch (10g) tended to shared more often with larger species (larger species towards the right side of figure, while (b) larger species such as the Northern Flicker (130g) tended to share more often with relatively smaller species on average (smaller species towards the left of figure). Note: Hairy Woodpeckers and Red-naped Sapsuckers mostly nest in live aspen, explaining their lower sharing with Red-breasted Nuthatch which uses primarily dead aspen (Martin 2014). (c) Greater

differences in mass between two species sharing a nest tree was associated with closer vertical distances between the two cavity entrances on the tree.

Figure 3. Partial regression plots showing residual frequency of nests in shared nest trees as a function of (a) snag density, (b) nest predation risk, and (c) woodpecker density in the previous year.

Figure 4. (a) Predicted daily nest success rate for nests in shared and unshared nest trees as a function of mean annual nest predation rates. (b) Mean annual nest predation rates by year. (c) Predicted daily nest success rate for nests in shared and unshared nest trees as a function of species body mass. Predictions are from the highest supported model and are based on mean values for all habitat covariates. Predictions for body mass are from a high nest predation year.

Figure A1. The proportion of nest trees shared by species. Species are organized from the smallest (Red-breasted Nuthatch – 10g) to the largest (Northern Flicker – 130g) species (a-j).

Figures:

Fig. 1:

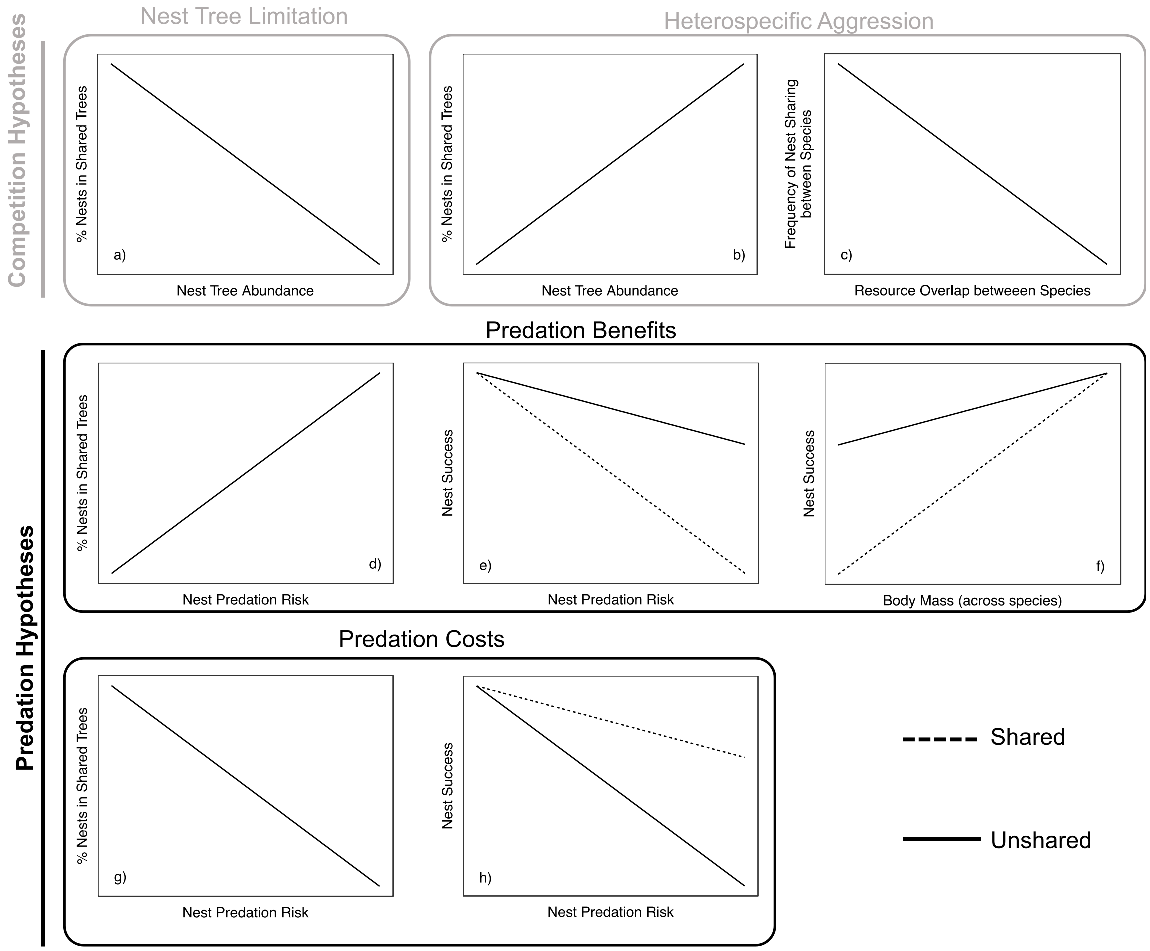


Fig. 2:

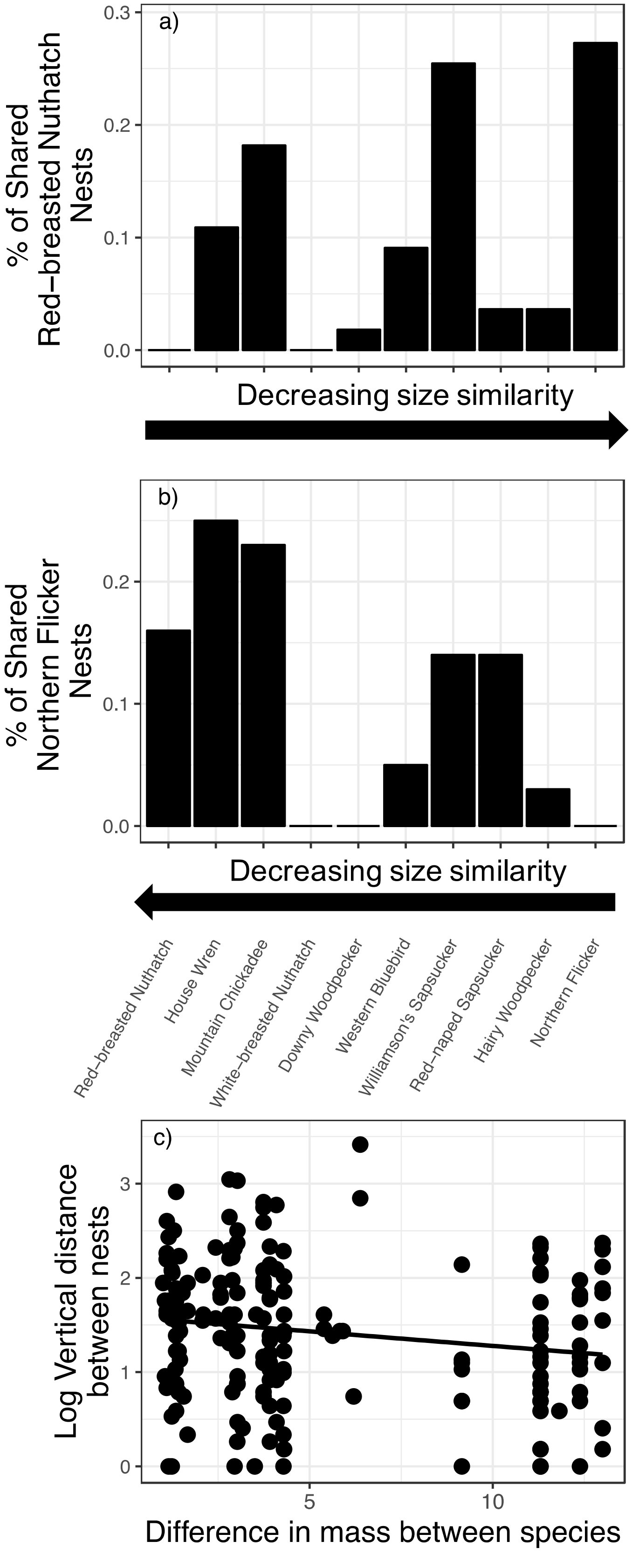

a)
% of Shared Red–breasted Nuthatch Nests
0.0
0.1
0.2
0.3
Decreasing size similarity
b)
% of Shared Northern Flicker Nests
0.0
0.1
0.2
Decreasing size similarity
Red–breasted Nuthatch
House Wren
Mountain Chickadee
White–breasted Nuthatch
Downy Woodpecker
Western Bluebird
Williamson's Sapsucker
Red–naped Sapsucker
Hairy Woodpecker
Northern Flicker
c)
Log Vertical distance between nests
0
1
2
3
5
10
Difference in mass between species

Fig. 3:

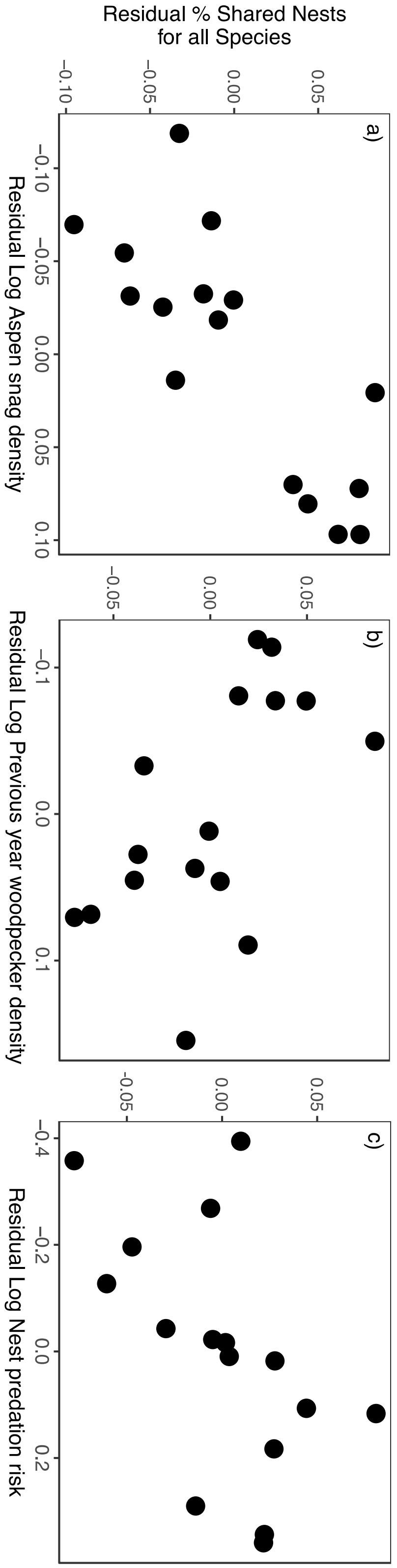

Residual % Shared Nests
for all Species
a)
b)
c)
−0.10
−0.05
0.00
0.05
0.10
Residual Log Aspen snag density
Residual Log Previous year woodpecker density
−0.1
0.0
0.1
Residual Log Nest predation risk
−0.4
−0.2
0.2

Fig. 4:

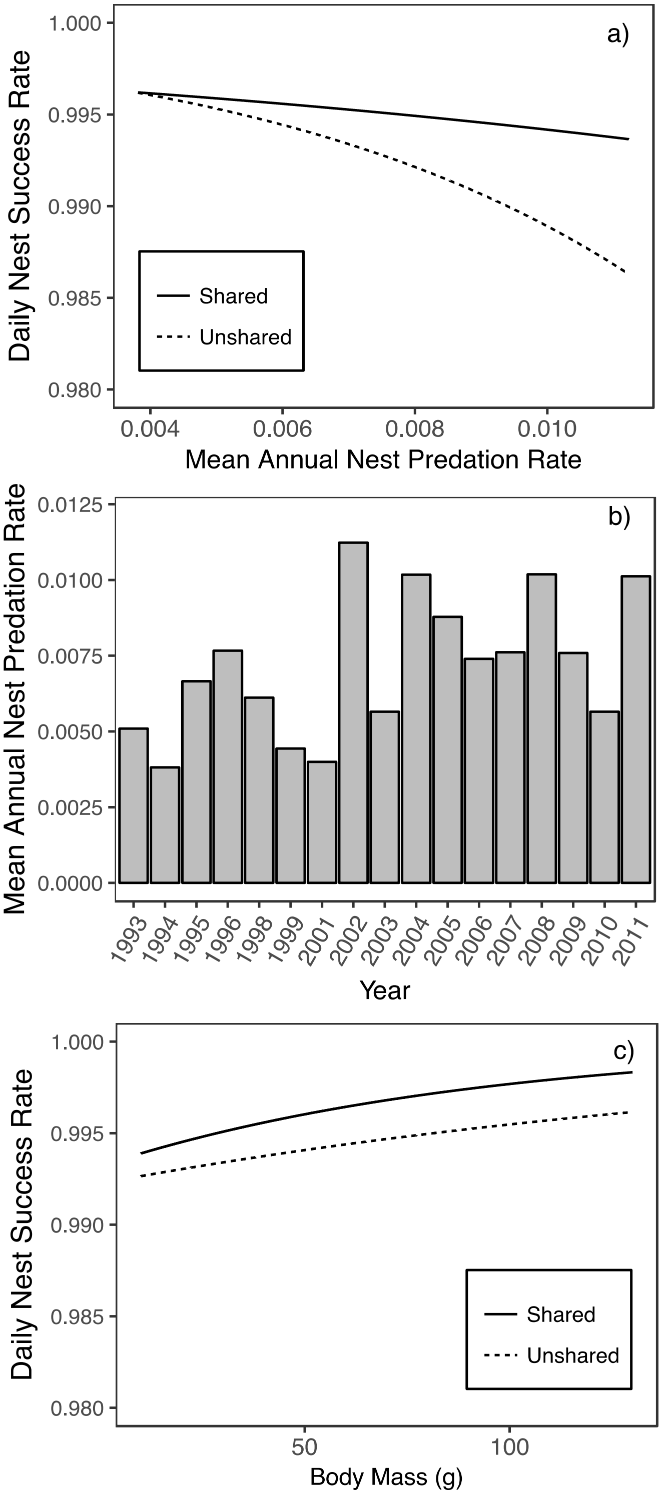
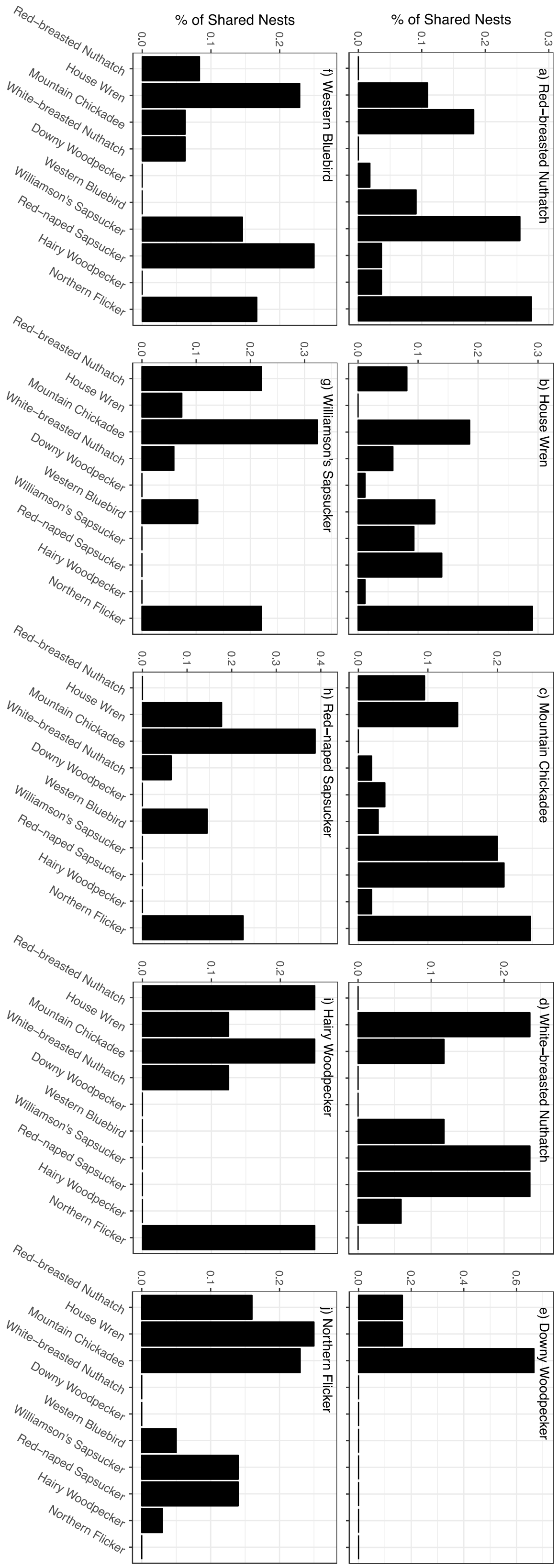

a)
Daily Nest Success Rate
1.000
0.995
0.990
0.985
0.980
Shared
Unshared
0.004
0.006
0.008
0.010
Mean Annual Nest Predation Rate
b)
Mean Annual Nest Predation Rate
0.0125
0.0100
0.0075
0.0050
0.0025
0.0000
1993
1994
1995
1996
1998
1999
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
Year
c)
Daily Nest Success Rate
1.000
0.995
0.990
0.985
0.980
Shared
Unshared
50
100
Body Mass (g)

Fig. S1:


a) Red–breasted Nuthatch
b) House Wren
c) Mountain Chickadee
d) White–breasted Nuthatch
e) Downy Woodpecker
f) Western Bluebird
g) Williamson's Sapsucker
h) Red–naped Sapsucker
i) Hairy Woodpecker
j) Northern Flicker
% of Shared Nests
% of Shared Nests
0.0
0.1
0.2
0.3
0.4
0.6
Red–breasted Nuthatch
House Wren
Mountain Chickadee
White–breasted Nuthatch
Downy Woodpecker
Western Bluebird
Williamson's Sapsucker
Red–naped Sapsucker
Hairy Woodpecker
Northern Flicker

CHAPTER 4: PARENTAL RESPONSES TO OFFSPRING SOLICITATION ARE INFLUENCED BY ENERGETIC CONSIDERATIONS

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Abstract:

Parents must balance the benefits of providing care to current young with costs to future reproduction. Offspring solicitation (begging) may help parents achieve this balance by signaling information about offspring needs. However, parental responsiveness to offspring begging varies dramatically across species. Understanding the causes of this variation is critical because the allocation of parental care between broods has major implications for lifetime fitness. Life history (adult survival or offspring predation rates) or ecological (food predictability or offspring need) differences among species may drive this variation, but comparative studies are lacking. Here, we measured parental feeding responses to begging calls broadcasted at nests of 17 songbird species at tropical and north temperate field sites. Overall, begging playback increased parental feeding rates, and responses varied across species. We used phylogenetic path analysis to test alternative hypotheses for the evolution of parental responsiveness to begging, and found little support for direct effects of adult survival and offspring predation risk on parental responses. In contrast, we found evidence that more unpredictable food availability and smaller nestling body size increased parental responsiveness across species. Ultimately, the evolution of parental responsiveness to offspring solicitation is largely driven by energetic needs of young.

Keywords: offspring solicitation; begging; provisioning; parental care; parent-offspring conflict; life history evolution

Introduction:

Parents must balance taking care of their young to increase current reproductive success versus taking care of themselves to increase future reproductive success (Williams 1966; Charlesworth 1994; Roff 2002). Offspring often provide signals to parents about their need for care that may help parents make decisions to achieve this balance (Godfray 1991; Godfray 1995). However, parental responses in overall provisioning vary among species (Clark & Lee 1998; Price 1998; Grodsinski & Lotem 2007; Tarwater et al. 2009; Haff & MacGrath 2011). In some species, parents provision broods substantially more with increased begging cues, but, in other species, begging intensity has little or no impact on parental provisioning. Given the ubiquity of offspring solicitation across avian and non-avian taxa, understanding the drivers of variation in parental responses to these signals is critical for determining the fitness consequences of parent-offspring communication. However, comparative studies are rare and the reason parental responsiveness to begging differs among species remains unclear.

One possibility is that parental responsiveness to offspring begging varies with longevity and the probability of future reproduction. In short-lived species, parental fitness is closely tied to the fitness of current young (Williams 1966; Charlesworth 1994, Roff 2002), so parents may respond to offspring begging by increasing provisioning (Kilner & Hinde 2008). In contrast, parents of longer lived species have a greater share of their lifetime fitness in future offspring (i.e. greater residual reproductive value; Williams 1966; Charlesworth 1994, Roff 2002) and parents may not increase provisioning in response to offspring begging may experience higher fitness in order to increase chances of reproducing in the future (Kilner & Hinde 2008). Thus, the evolution of parental responsiveness to offspring begging may be shaped by variation in adult survival among species (*future reproduction hypothesis*; Fig. 1A).

Offspring predation risk may also influence parental responsiveness to begging in two ways. First, parental provisioning activity can help predators locate young (Skutch 1945; Martin et al. 2000; Muchai and DuPleiss 2005), and parents may mitigate predation risk by providing care based on perceived safety rather than offspring begging cues. Consequently, species with greater offspring predation rates may have evolved lower responsiveness to begging than species that experience little offspring predation (*reduced visitation hypothesis*; Fig. 1B). Second, offspring may have evolved to leverage the fact that begging cues can attract predators to "blackmail" parents to provide more care (*blackmail hypothesis*; Fig. 1B; Zahavi 1977; Haff & MacGrath 2011; Thompson et al. 2013). This strategy should be more effective in species with greater offspring predation rates and, so, these species may evolve greater responsiveness to begging than species with lower predation rates.

A third hypothesis centers on offspring energetic needs (*offspring need hypothesis*; Fig. 1C). If offspring have high energetic expenditures from high mass-specific metabolism and low capacity to store energy (e.g., small body mass), the time between offspring first begging and beginning to suffer costs may be relatively short. In contrast, offspring with lower mass-specific metabolic rate and greater ability to store energy (e.g., large body mass) may be able to beg for a much longer time before lack of care yields costs. If energy requirements of offspring are important, parents should be less responsive in species with larger rather than smaller nestlings (Grodsinski & Lotem 2007).

A final hypothesis centers on availability or predictability of food resources (*environmental predictability hypothesis*; Fig. 1D; Caro et al. 2016). A meta-analysis showed that bird species with greater levels of brood reduction from poor unpredictable environmental conditions preferentially fed offspring in better condition rather than nest mates that begged most intensely (Caro et al. 2016). Since food conditions could deteriorate at any time, such species maximize their chance of at least one offspring surviving even if the odds some young will die also increase. Similarly, species that experience more unpredictable food availability may be less responsive to begging than species with more constant food availability because the reproductive value of any current brood is relatively low given that food supply could deteriorate (Martin 1987). Yet the idea that species with predictable food supply (i.e. low brood attrition) adjust total provisioning based on offspring solicitation cure is untested.

Here we used a playback experiment to increase the intensity of begging cues at nests in 17 species of tropical and north temperate songbirds and examined parental responses in feeding activity. We compared parental responsiveness across species differing in adult survival, nest predation rates, nestling body mass, and brood attrition rates and used phylogenetic path analysis to test the relative importance of each alternative hypothesis (Fig. 1).

Methods:

Data collection:

We studied 11 songbird species in primary tropical montane forest at Kinabalu Park in Sabah, Malaysia from 2009-2019. We also studied 6 species of songbird from mixed temperate forest in central Arizona, USA from 1987-2017. We found and monitored nests between February and June in Malaysia and April and July in Arizona. We recorded brood size and survival of young from hatching until fledge to determine nest predation rates. We calculated brood attrition rates as the percentage of nests where at least one young died prior to fledging. We also weighed nestlings on the day when the primary flight feathers begin to push through their sheaths (hereafter pin break).

We used standard effort mist netting along with resighting of color-banded birds to estimate annual apparent adult survival (Martin et al. 2015, 2017). At both sites, we used 12 nets at each netting plot and sampled each plot 3 times over the course of the breeding season. We opened nets for 6 hours each day beginning at sunrise. Birds were marked with aluminum bands with unique identifiers and three plastic color bands in a unique arrangement to facilitate identifying individuals through resighting. Birds were resighted opportunistically throughout each study area by nest searchers.

Begging calls for each species were recorded on pin break in the field using a digital recorder (PMD 661 by Marantz, Chatsworth, CA, USA) and small lapel microphone (model AT831C; Audio-Technica, Tokyo, Japan). The microphone was placed exactly 15 cm away from the inside edge of the nest cup. We ensured all settings (e.g. gain) were identical on the recorder for each recording. All recordings were made on nests with typical brood sizes for each species and at a standardized developmental stage (pin break) to allow comparisons across species.

Playback Experiment:

We conducted begging playback experiments in 2016-2018 in Malaysia and 2016-2017 in Arizona. Within 1-2 days of pin break day, we placed small camouflaged speakers (Groove Cube by WowWee Group Limited, Hong Kong) immediately adjacent to nests and set up a video camera to film parental behavior. We first filmed nests for at least 80 mins without the speakers broadcasting anything to allow parents to acclimatize to the presence of the speakers. Then we played either begging call recordings from the same species or white noise as a control for 80 mins. We constructed playback recordings with 10 seconds of sound (either begging or white noise) followed by 50 secs of silence each minute to simulate bouts of begging. Each playback recording consisted of begging recordings from at least 4 unique nests for each species. We alternated whether we played the begging recordings or control recordings first for each nest in a species. After 80 mins the recording automatically switched treatments (i.e. the control if the begging recording was played first). All recordings were played at typical volumes for each species as measured by a sound level meter at 15 cm without obstructions (Model 407730, Extech Instruments Corporation). The average volume of control and begging recordings were similar. All playback experiments began at about the same time each day (0730-0930).

Statistical Analyses:

Nest predation rates during the nestling period were estimated using the logistic exposure method (Shaffer 2004). We included species as a fixed effect and included nested random intercepts for year within site.

To obtain a measure of parental responsiveness to experimental begging playback for each species, we calculated total feeding rates for treatment and control periods and divided them by the average feeding rates on pin break for each species to allow for standardized comparisons across species. We modelled feeding rate using separate linear mixed effect models for each species. We used a fixed factor indicating whether begging or control noises were being broadcast. We also included fixed effect terms to control for age of the young relative to pin break and the number of young in the nest (brood size). We used a random intercept term to account for variation between each nest. We repeated the experiment on several nests in subsequent days and accounted for variation between films by including random intercept for film within nest. The coefficient for begging playback estimated for each species was used as a measure of parental responsiveness to begging in all subsequent comparative analyses.

We used a linear mixed effect model to test for the average response to experimental playback. We included a fixed effect for begging playback (vs. control) and a nested random effect to account for variation among sites, species and nests.

We examined the association of parental responsiveness with adult survival rate, nest predation rate, attrition rate, and nestling mass using phylogenetic generalized least squares (PGLS) in the package 'ape' (Paradis & Schliep 2018). Because one species (Chestnut-crested Yuhina) was a high leverage outlier (Cook's Distance = 0.812), we report all results with and without this outlier species included. These models describe correlations between the variables of interest, but do not allow inference on the causal processes that created the data or account for causal relationships between the variables. We log-transformed adult and nestling body mass to meet model assumptions.

To determine the causal drivers of parental responsiveness to begging, we used phylogenetic path analysis (PPA; von Hardenberg & Gonzalez-Voyer 2013). PPA uses the d-separation method to test the plausibility that a causal model created the observed data and to compare the relative support of mulitple models using an information theoretic approach. We developed 15 possible models that described the direct effects of annual adult survival rate, nest predation rate, brood attrition rate, and nestling mass on parental responsiveness to begging playback as well as likely causal relationships between these variables (Fig S1). For example, since nestling mass and nest predation rate are both likely influenced by adult mass (Mouton & Martin 2019), each model describes a direct effect of adult mass on nestling mass and nest predation rate. We tested each of k conditional independencies of each model using phylogenetic least-squares regression (PGLS), implemented in the package 'phylopath' (van der Bijl 2018). We report the plausibility of each causal model based on Fisher's C statistic, which follows a chi-squared distribution with 2k degrees of freedom. We used the C statistic Information Criterion with a correction for small sample sizes (CICc) to rank and compute the probability of each causal model and variable given the data and the candidate model set (CIC weight; Anderson et al. 2000; von Hardenberg & Gonzalez-Voyer 2013).

Phylogenetic trees were acquired from birdtree.org (Jetz et al. 2012) using the Hackett backbone (Hackett et al. 2008). We sampled a distribution of 1000 trees and produced majority-rules consensus trees using program Mesquite (Maddison & Maddison 2011).

Results:

We broadcast begging playback at an average of 7.2 nests per species (range = 5 – 12). Parents generally increased feeding visits to their nests when experimental begging vocalizations were being broadcast relative to controls (linear mixed-effects model: $\beta = 0.246$, $P < 0.001$), but the magnitude of responses differed among species. Average parental responses to experimental begging did not differ between the two field sites (PGLS: $\beta = 0.089$, $P = 0.355$). Mean parental responsiveness to begging did not differ among species with variation in adult survival (Fig. 2A; PGLS: $\beta = 0.252$, $P = 0.663$; outlier removed: $\beta = 0.356$, $P = 0.364$; Fig. 2A) or nestling predation rates (Fig. 2B; PGLS: $\beta = -0.327$, $P = 0.921$; outlier removed: $\beta = 1.586$, $P = 0.479$; Fig. 2B). However, species with smaller nestling mass were more responsive to begging than larger species (Fig. 2C; PGLS: $\beta = -0.308$, $P < 0.037$; outlier removed: $\beta = -0.259$, $P = 0.009$; Fig. 2D). Species with greater brood attrition were more responsive to begging than species with less brood attrition, but only after removing the high leverage outlier (Chestnut-crested Yuhina; Cook's D = 0.815) from the data (Fig. 2D; PGLS: $\beta = 0.692$, $P = 0.355$; outlier removed: $\beta = 2.06$, $P = 0.006$; Fig. 2C).

Numerous causal models could have plausibly created the results (Table 1). Direct effects of nestling mass (CICc weight = 0.831; outlier removed: 0.621) and nestling attrition (CICc weight =0.155; outlier removed: 0.899) on parental responsiveness to begging were strongly supported, whereas direct effects of adult survival (CICc weight = 0.008; outlier removed: 0.124), and nestling predation rates (CICc weight = 0.010; outlier removed: 0.114) were less supported. The only model within < 2 ΔCICc with all species included predicted a negative effect of nestling mass (Fig. 3B). The top model with Chestnut-crested Yuhina excluded predicted a negative effect of nestling mass and a positive effect of brood attrition on parental responsiveness to begging (Fig. 3C).

Discussion:

Parental responsiveness to offspring solicitation behavior varies dramatically across species, but the drivers of this variation are unclear and comparative studies are rare. Using standardized field methods across species, we show that variation in parental responsiveness to begging differs dramatically across species and appears to be driven largely by variation in ecological factors related to the energetic needs of young rather than residual reproductive value or average predation risk. Species with larger nestlings and higher levels of brood attrition were more responsive to offspring begging calls (Fig. 2). Furthermore, our data were highly consistent with causal hypotheses depicting direct effects of nestling size and brood attrition on parental responsiveness.

In support of the *offspring need hypothesis*, species with smaller mass were more responsive to begging. Our comparative results agree with an experiment in House Sparrows which suggested that parental responsiveness balanced the risk of wasting time returning too soon to feed already satiated young against the risk of failing to feed young in need (Grodsinski & Lotem 2007). Larger nestling body sizes are associated with increased energetic stores and reduced mass specific metabolism (Ton & Martin 2015), and may allow longer intervals without being fed with minimal consequences for offspring survival. In contrast, parents may view begging calls with greater urgency in smaller species with fewer energetic stores and higher mass specific metabolism. Overall, parental responsiveness to begging seems to be greater in species where begging is more likely to signal imminent survival costs for young based on energy requirements.

Increased begging intensity may also signal more dire need in species with more unpredictable food resources and may help explain our result that species with higher levels of brood attrition tend to be more responsive to begging calls. If food is currently abundant and increased provisioning is possible, species with more unpredictable food supplies may respond to increased begging signals to decrease the odds that young die if conditions deteriorate in the future. This result contrasts with the *environmental predictability hypothesis* and is surprising in light of previous work that has shown that in species with relatively high levels of brood attrition, parents do not preferentially feed individual nestlings with higher begging intensity (Caro et al. 2016). One possible explanation for this discrepancy is that when deciding which offspring to provision within the current brood, parents are able to assess the likely outcome for each individual. In contrast, parents are unable to directly assess the likely outcomes of current vs. future broods. Indeed, even among long-lived species that on average should expect to have many breeding attempts in the future, no parent knows whether conditions will improve in the future or if it will be killed by a predator or other extrinsic causes. Due to this uncertainty, parents may increase total provisioning in response to increased begging to increase the survival probability of their current offspring. Ultimately, increased parental responsiveness to begging in species with high brood attrition may reflect parents' efforts to maximize the likelihood that current young survive.

Given that parents with greater likelihood of reproducing in the future should experience more intense parent-offspring conflict than parents that are unlikely to breed again in the future (Kilner & Hinde 2008), our result that adult survival was not a major driver of variation in parental responsiveness across species was also surprising. Nonetheless our results are bolstered by single species studies that used similar methods (Clark & Lee 1998; Price 1998; Tarwater et al. 2009; Haff & MacGrath 2011). For example, the Slaty Antshrike has high adult survival, but was highly responsive to begging playback (Tarwater et al. 2009). Meanwhile, the relatively short-lived Red-winged Blackbird did not increase provisioning with a similar playback experiment (Clark & Lee 1998). Residual reproductive value may still place a ceiling on the total amount of care parents will provide (Martin 2014), but in the short term, does not seem to strongly influence parental responses to offspring behavior.

Offspring predation risk was not a major driver of parental responsiveness to begging across species as we found little support for either the *reduced visitation hypothesis* or the *blackmail hypothesis*. Previous single species studies have also given mixed results. Some bird species with relatively high nest predation rates were highly responsive to experimentally augmented nestling begging calls (Price 1998; Tarwater et al. 2009). Yet other species with similarly high predation rates showed very little parental responsiveness (Clark & Lee 1998). Moreover, a cavity nesting species with very low nest predation rates readily responded to increased begging playback (Hinde & Kilner 2007). Sensory biases among common nest predators may determine the importance of offspring predation risk as a driver of parental responsiveness to begging across species. In both Malaysia and Arizona, common nest predators are able to cue into nests using both auditory and visual cues and, so, selection for faster parental feeding responses to silence loud begging may be offset by selection for reduced visitation. Communities dominated by nest predators with either auditory or visual sensory biases may face more directional selection on parental responsiveness to begging. Nonetheless, offspring predation risk was not a major factor at our north temperate or tropical site suggesting our results may be generalizable to other communities as well.

Other ecological traits may also drive variation in parental responsiveness to offspring begging. For example, species that raise young cooperatively in groups might be expected to be more responsive overall because the costs of increasing provisioning are divided among multiple individual caregivers. Unfortunately, our study only included 2 species that are obligate cooperative breeders so we lack the ability to test this hypothesis directly. However, cooperative breeding may not have strong effects on parental responsiveness. Mountain Wren-Babblers (MWBA; *Napothera crassa*) with above average levels of attrition were among the more responsive species. However, Chestnut-Crested Yuhinas (CCYU; *Yuhina everetti*) are cooperative breeders with high levels of brood attrition, showed very little response to increased begging cues, and were a high leverage outlier in our analysis (Fig. 2). Since non-parental caregivers in cooperatively breeding species are less related to young than parents, it’s possible that reduced costs associated with cooperative breeding may be offset by reduced benefits from providing care. Future studies could examine how variation in group size as well as differing degrees of relatedness within cooperatively breeding species influences responsiveness to begging.

The level of parental care provided to offspring is a major aspect of life history strategies across taxa with critical implications for fitness (Williams 1966; Charlesworth 1994; Roff 2002) Offspring can influence the level of parental care they receive using solicitation displays, but parental responsiveness to solicitation displays varies across species. Here we provide evidence that the energetic needs of offspring and environmental predictability drive this variation across diverse species. In contrast, we found little evidence that variation among species in adult survival or nestling predation rates drive the evolution of parental responsiveness to offspring begging. The widespread expression of offspring solicitation behaviors across taxa begs for studies examining the evolutionary drivers of parental responsiveness in other contexts.

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References:

Anderson, DR, Burnham, KP, Thompson, WL. 2000 Null hypothesis testing: problems, prevalence, and an alternative. *J. Wildl. Manag.* **64**, 912-923.

Caro, SM, Griffin, AS, Hinde, CA, West, SA. 2016 Unpredictable environments lead to the evolution of parental neglect in birds. *Nature Comm.* **7**, 10985.

Charlesworth, B. 1994 *Evolution in age-structured populations,* Cambridge, UK: Cambridge University Press.

Clark, AB, Lee, WH. 1998 Red-winged blackbird females fail to increase feeding in response to begging call playbacks. *Anim. Behav.* **56**, 563-570.

Godfray, HCJ. 1991 Signalling of need by offspring to their parents. *Nature* **352**, 328-330.

Godfray, HCJ. 1995 Signaling of need between parents and young: parent-offspring conflict and sibling rivalry. *Am. Nat.* **146**, 1-24.

Grodzinski, U, Lotem, A. 2007 The adaptive value of parental responsiveness to nestling begging. *Proc. R. Soc. B* **274**, 2449-2456.

Hackett, SJ, *et al.* 2008 A phylogenomic study of birds reveals their evolutionary history. *Science*, **320**, 1763-1768.

Haff, TM, Magrath, RD. 2011 Calling at a cost: elevated nestling calling attracts predators to active nests. *Biol. Lett.* **7**, 493-495.

Kilner, RM, Hinde, CA. 2008 Information warfare and parent–offspring conflict. *Adv. St. Behav.* **38**, 283-336.

Jetz, W., Thomas, GH, Joy, JB, Hartmann, K, Mooers, AO. 2012 The global diversity of birds in space and time. *Nature* **491**, 444-448.

Kilner, RM, Hinde, CA. 2012 Parent-offspring conflict. In *The evolution of parental care*, pp. 119-132. Oxford, UK: Oxford University Press.

Maddison, WP, Maddison, DR. 2011 Mesquite: a modular system for evolutionary analysis. Version 2.75.

Martin, TE. 1987 Food as a limit on breeding birds: A life-history perspective. *Ann. Rev. Ecol. Sys.* **18**, 453-487.

Martin, TE, Scott, J, Menge, C. 2000 Nest predation increases with parental activity: separating nest site and parental activity effects. *Proc. R. Soc.* B **267**, 2287-2293.

Martin, TE, Oteyza, JC, Boyce, AJ, Lloyd, P, Ton, R. 2015 Adult mortality probability and nest predation rates explain parental effort in warming eggs and embryo development time. *Am. Nat.* **186**, 223-236.

Martin TE, Riordan, MM, Repin, R, Mouton, JC, Blake, W.M. 2017 Apparent annual survival estimates of tropical songbirds better reflect life history variation when based on intensive field methods. *Glob. Ecol. Biogeogr.* **26**, 1386-1397.

Mouton, JC, Martin, TE. 2019 Nest structure affects auditory and visual detectability, but not predation risk, in a tropical songbird community. *Func. Ecol.* **00**,1– 9.

Muchai, M, Plessis, MAD. 2005 Nest predation of grassland bird species increases with parental activity at the nest. *J. Avian Biol.* **36**, 110-116.

Paradis E, Schliep K. 2018 ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics* **35**, 526-528.

Price, K. 1998 Benefits of begging for yellow-headed blackbird nestlings. *Anim. Behav.* **56**, 571-577.

Roff, DA. 2002 *Life history evolution*. Boston, MA: Springer US.

Shaffer, TL. 2004 A unified approach to analyzing nest success. *Auk* **121**, 526-540.

Skutch, AF. 1945 Incubation and nesting periods of Central American birds. *Auk* **62**, 8-37.

Tarwater, CE, Kelley, JP, Brawn, JD. 2009 Parental response to elevated begging in a high predation, tropical environment. *Anim. Behav.* **78**, 1239-1245.

Thompson, AM, Raihani, NJ, Hockey, PAR, Britton, A, Finch, FM, Ridley, AR. 2013 The influence of fledgling location on adult provisioning: a test of the blackmail hypothesis. *Proc. R. Soc. B* **280**, 20130558.

Ton, R, Martin, TE. 2016 Metabolism correlates with variation in post-natal growth rate among songbirds at three latitudes. *Func. Ecol.* **30**, 743-748.

Trivers, RL. 1974 Parent-offspring conflict. *Integr. Comp. Biol.* **14**, 249-264.

von Hardenberg A, Gonzalez-Voyer, A. 2013 Disentangling evolutionary cause-effect relationships with phylogenetic confirmatory path analysis. *Evolution* **67**, 378-387.

van der Bijl, W. 2018 phylopath: Easy phylogenetic path analysis in R. *PeerJ*, **6**, e4718. (doi:10.7717/peerj.4718, R package version 1.1.1)

Williams, GC. 1966 Natural selection, the costs of reproduction, and a refinement of Lack's principle. *Am. Nat.* **100**, 687-690.

Zahavi, A. 1977 Reliability in communication systems and the evolution of altruism. In *Evolutionary ecology*, pp. 253-259. London, UK: Macmillan.

Tables:

Table 1: Results from phylogenetic path analysis indicating the variables posited to have direct causal effects on parental responsiveness to begging for each model. *k* is the number of conditional independencies tested for each model and *q* indicates the number of parameters estimated. *C* is Fischer's C statistic. Low *p*-values (e.g. $p<0.05$) indicate models could not have plausibly created the data. Models are ordered based on the C statistic Information Criterion with a correction for small sample sizes (CICc). We also report the difference in CICc between models (ΔCICc) and the likelihood (*l*) and CICc weight of each model. We show all models within 10 ΔCICc of the top model. All causal models are depicted graphically in the supplementary material (Fig. S1).

A) All species included:

Model	Variables	*k*	*q*	*C*	*p*	CICc	ΔCICc	*l*	weight
D	Nestling Mass	16	20	37.49	0.232	-90.51	0.00	1.000	0.826
C	Brood Attrition	16	20	40.86	0.135	-87.13	3.37	0.185	0.153
B	Nest Predation	16	20	46.54	0.047	-81.45	9.05	0.011	0.009
A	Adult Survival	16	20	47.15	0.041	-80.84	9.66	0.008	0.007
J	Brood Attrition Nestling Mass	15	21	33.22	0.313	-78.77	11.73	0.003	0.002
G	Nestling Mass Adult Survival	15	21	34.04	0.279	-77.95	12.55	0.002	0.002
I	Nestling Mass Nest Predation	15	21	34.70	0.254	-77.29	13.21	0.001	0.001

B) Chestnut-crested Yuhina excluded:

Model	Variables	*k*	*q*	*C*	*p*	CICc	ΔCICc	*l*	weight
J	Nestling Mass Brood Attrition	15	21	35.13	0.238	-54.86	0.00	1.000	0.417
C	Brood Attrition	16	20	45.93	0.053	-54.06	0.80	0.669	0.279
M	Nestling Mass Brood Attrition Adult Survival	14	22	30.79	0.326	-51.70	3.15	0.206	0.086
H	Brood Attrition Nest Predation	15	21	38.52	0.137	-51.47	3.39	0.183	0.076
D	Nestling Mass	16	20	48.52	0.031	-51.47	3.40	0.183	0.076
N	Nestling Mass Brood Attrition Nest Predation	14	22	33.70	0.211	-48.79	6.06	0.048	0.020
F	Brood Attrition Adult Survival	15	21	42.46	0.065	-47.53	7.32	0.026	0.011

Figure Legends:

Fig. 1: Hypotheses explaining why species differ in parental responsiveness to offspring solicitation (begging) calls. **(A)** The *future reproduction hypothesis* predicts species with greater annual adult survival rate will be less responsive to offspring begging. **(B)** The *reduced visitation hypothesis* (i; dashed line) predicts that species with higher mean nest predation rates should be less responsive to offspring begging calls. In contrast, the *blackmail hypothesis* predicts species with higher nest predation rates should be less responsive to offspring begging (ii; solid line). **(C)** The *offspring need hypothesis* predicts species with greater nestling mass will be less responsive to offspring begging calls. **(D)** The *environmental predictability hypothesis* predicts that species with greater brood attrition should be less responsive to offspring begging calls.

Fig. 2: Partial residual plots showing relationships between parental responsiveness to begging and **(A)** annual adult survival rate, **(B)** nest predation rate during the nestling stage, **(C)** nestling mass, and **(D)** brood attrition. Data from the tropical Malaysia site are depicted in blue and data from the north temperate Arizona, USA site are depicted in orange. The open symbol depicts Chestnut-crested Yuhina, a high leverage outlier (see *Statistical Analyses* for details).

Fig. 3: (**A)** Conceptual framework illustrating hypothesis to be tested using phylogenetic path analysis. **(B)** The best supported model and only model within <2 ΔCICc depicted with standardized path coefficients for all relationships. Gray arrows depict relationships included in all models.

Fig. 1:

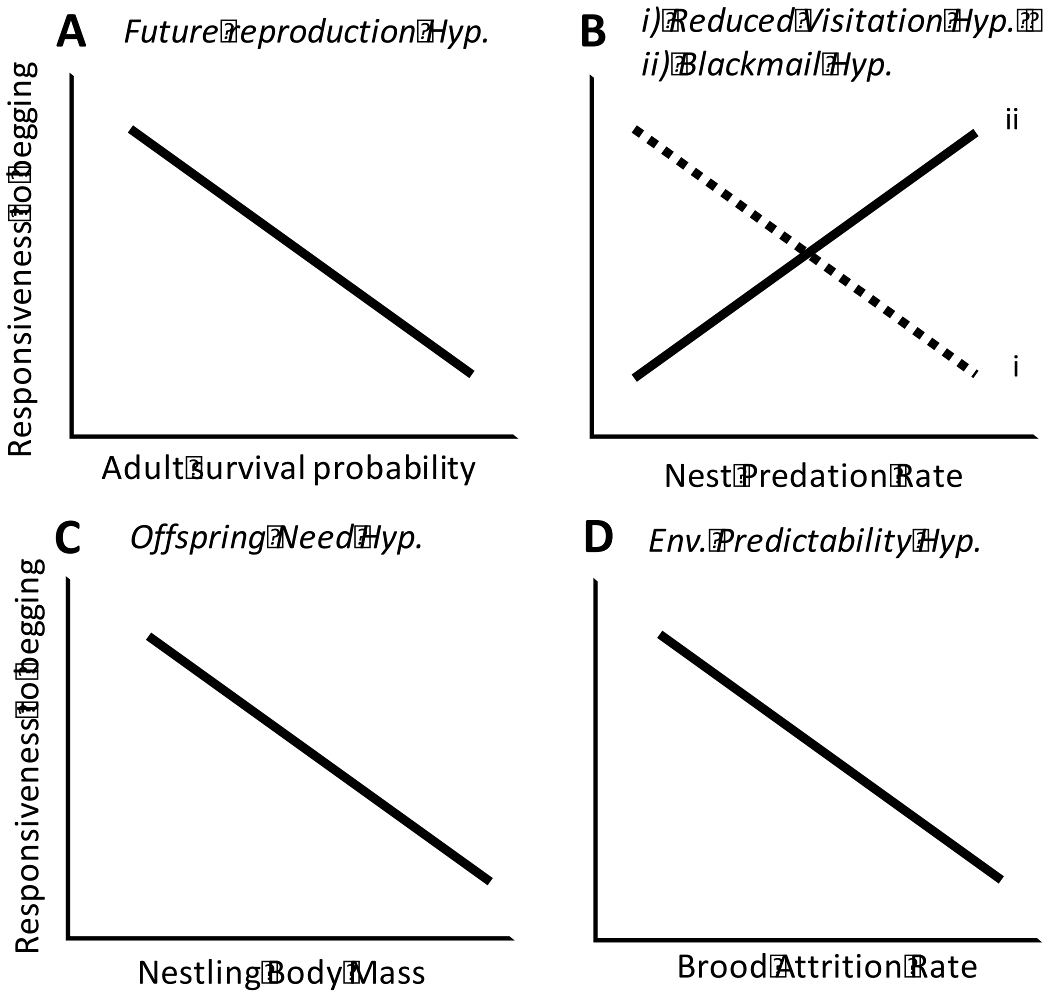

A
Future reproduction Hyp.
Responsiveness to begging
Adult survival probability
B
i) Reduced Visitation Hyp.
ii) Blackmail Hyp.
ii
i
Nest Predation Rate
C
Offspring Need Hyp.
Responsiveness to begging
Nestling Body Mass
D
Env. Predictability Hyp.
Brood Attrition Rate

Fig. 2:

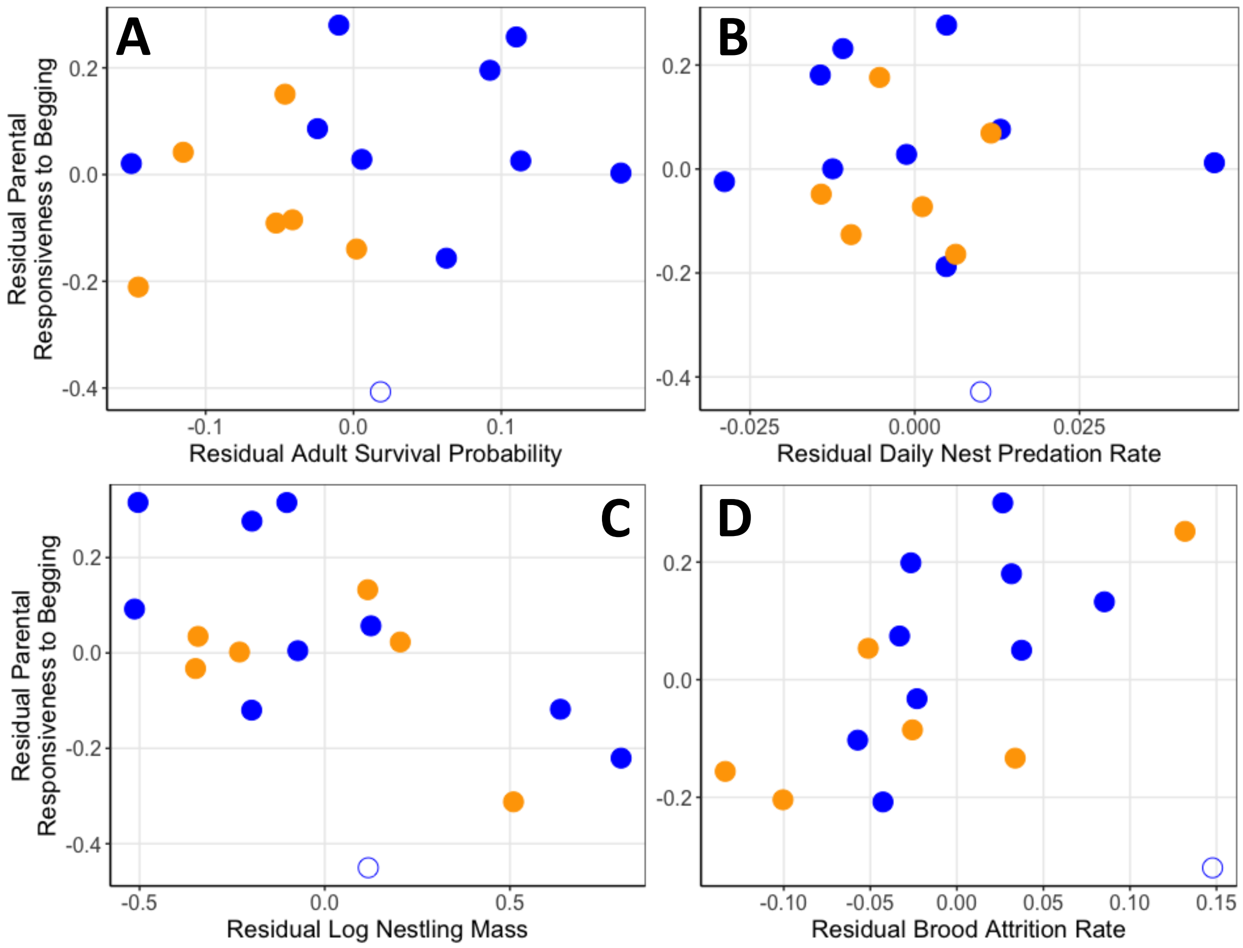
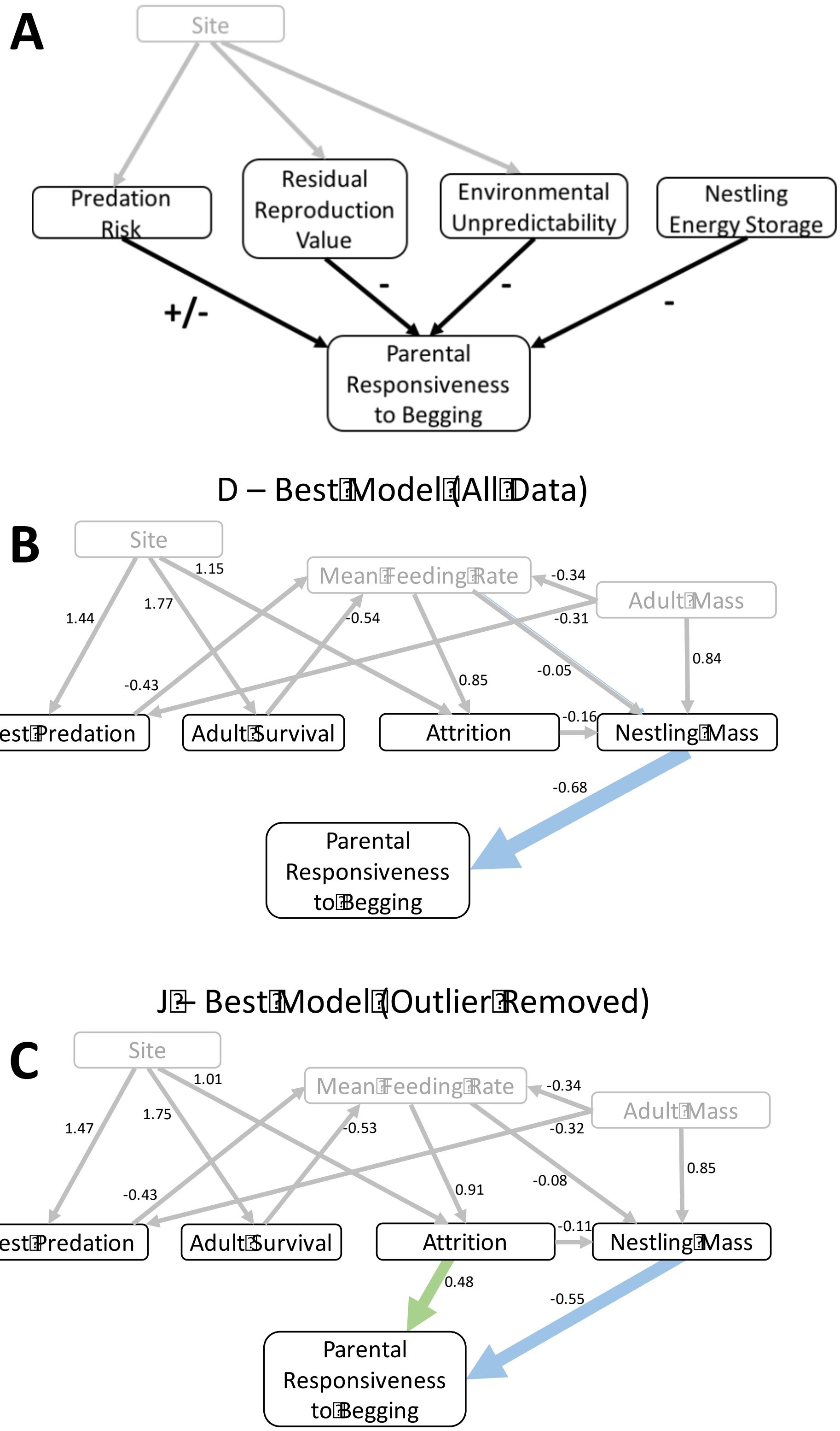

A
B
C
D
Residual Parental Responsiveness to Begging
Residual Adult Survival Probability
Residual Daily Nest Predation Rate
Residual Log Nestling Mass
Residual Brood Attrition Rate
0.2
0.0
-0.2
-0.4
-0.1
0.0
0.1
-0.025
0.000
0.025
-0.5
0.5
-0.10
-0.05
0.00
0.05
0.10
0.15

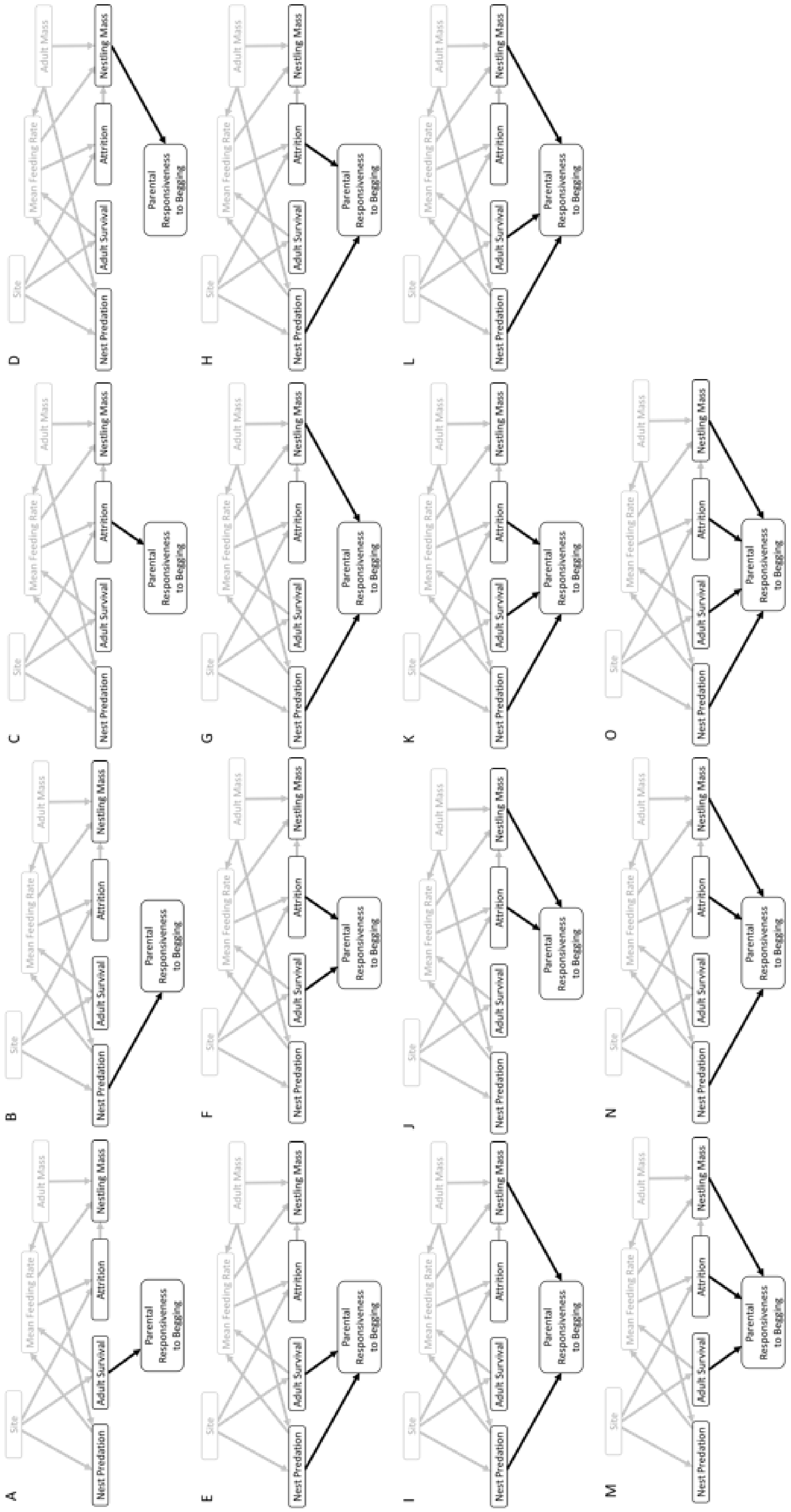
Fig. 3:


A
Site
Predation Risk
Residual Reproduction Value
Environmental Unpredictability
Nestling Energy Storage
+/-
-
-
-
Parental Responsiveness to Begging
D – Best Model (All Data)
B
Site
1.15
1.44
1.77
Mean Feeding Rate
-0.34
Adult Mass
-0.54
-0.31
-0.43
0.85
-0.05
0.84
-0.16
Nest Predation
Adult Survival
Attrition
Nestling Mass
-0.68
Parental Responsiveness to Begging
J – Best Model (Outlier Removed)
C
Site
1.01
1.47
1.75
Mean Feeding Rate
-0.34
Adult Mass
-0.53
-0.32
-0.43
0.91
-0.08
0.85
-0.11
Nest Predation
Adult Survival
Attrition
Nestling Mass
0.48
-0.55
Parental Responsiveness to Begging

Supplementary Material:

Fig. S1: Full set of causal models tested using phylogenetic path analysis. Gray arrows depict relationships included in all models.

Fig. S1:



A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
Site
Mean Feeding Rate
Adult Mass
Nest Predation
Adult Survival
Attrition
Nestling Mass
Parental Responsiveness to Begging

CHAPTER 5: NEST STRUCTURE AFFECTS AUDITORY AND VISUAL DETECTABILITY, BUT NOT PREDATION RISK, IN A TROPICAL SONGBIRD COMMUNITY

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Abstract:

1. Offspring mortality varies dramatically among species with critical demographic and evolutionary ramifications, yet the causes of this variation remain unclear. Nests are widely used for breeding across taxa and thought to influence offspring mortality risk. Traditionally, more complex, enclosed nest structures are thought to reduce offspring predation by reducing the visibility of nest contents and muffling offspring sounds compared to open nests. Direct tests of the functional bases for nest structure influences on predation risk are lacking.
2. We used experiments and 10 years of observational data to examine how nest structure influences nest predation risk in a diverse community of tropical songbirds. First, we examined how nest size was related to nest structure and nest predation rates across species. Second, we assessed how nest structure influences the detectability of nestling begging calls both in field and laboratory settings. Finally, we examined how the acoustic properties of different nest structures influence nest predation risk. Specifically, we experimentally broadcast begging calls from open and enclosed nests to determine how auditory cues and nest structure interact to affect predation on plasticine and quail eggs. We also tested whether nest structure was associated with differences in nest predation rates between the incubation (no begging cues) and nestling (begging cues) stages.
3. We found that enclosed nests are larger than open nests after accounting for adult size, and larger nests had increased predation rates. Moreover, enclosed nests did not consistently alter nestling begging calls in ways that reduce the likelihood of predation compared to open nests. Indeed, begging cues increased predation rates for enclosed but

not open cup nests in our playback experiment, and nest predation rates showed greater increases after hatching in enclosed than open cup nests.

4. Ultimately, enclosed nests do not necessarily provide greater predation benefits than open nests in contrast to long standing theory.

Keywords: nest structure, predation, enclosed, dome, open cup, acoustics, offspring solicitation, begging

Introduction:

Predation is a major source of mortality and can have important consequences for individual fitness and population dynamics across taxa. Mortality during vulnerable early life stages can have especially large effects on populations, yet offspring predation rates vary dramatically across species (Eckert 1987; Promislow & Harvey 1990; Martin 1992; Gosselin & Qian 1997; Martin et al. 2017). The wide diversity of nests and other shelters provided by parents for young offspring may help explain this variation. For example, more complex, enclosed nest structures are often thought to reduce the detectability of nest contents to predators compared with simpler, more open nests (invertebrates: Manicom, Schwarzkopf, Alford, & Schoener 2008; amphibians: Orizaola & Braña 2003; reptiles: Rand & Dugan 1983; birds: Mainwaring, Reynolds, & Weidinger 2015). This idea is long-standing and intuitive: a more enclosed nest structure should hide nest contents from visual detection by a predator and dampen sounds coming from young in the nest relative to an open cup nest. Yet, direct tests of the predation benefits of enclosed relative to open nests are rare.

In songbirds, enclosed nests (constructed with a roof and sides) are thought to reduce nest predation risk relative to open cup nests (exposed from above and on the sides; Wallace 1889; Nice 1957; Oniki 1985; Collias 1997; Hall, Street, Auty, & Healy 2015), but empirical evidence for such benefits is equivocal. First, if enclosed nests strongly increase reproductive success, then we would expect them to be the dominant nest type among songbirds. However, open nests are more common than enclosed nests across songbird species even though enclosed nests are the ancestral trait for the clade (Martin et al. 2017; Price & Griffith 2017; Fang, Tuanmu, & Hung 2018). Second, a recent global comparison across species found that regions with higher average nest predation rates did not have more enclosed than open nesting species and suggested that thermal rather than predation functions may be more important (Martin et al. 2017). Finally, experimental studies have also yielded variable (Møller 1989) or non-significant (Loiselle & Hoppes 1983) differences in nest predation rates between man-made nests with and without roofs. Notably, functional studies of nest structure's effects on nest detectability and predation rates are lacking.

Nest structure may influence nest detectability in more complex ways than commonly suggested. While eggs and young may be concealed in enclosed nests, the addition of a roof and walls may also result in larger nest size which can increase the likelihood that visually oriented predators detect the nest (Snow 1978; Møller 1990; Biancucci & Martin 2010). Moreover, sound from nestling begging is thought to influence predation risk and the roof and walls of enclosed nests might alter the sound of begging young which could influence the likelihood it is detected by predators (Haskell 1994; Leech & Leonard 1997; Briskie, Martin, & Martin 1999; Lampe, Dabelsteen, Larsen, & Pedersen 2004; Mennill & Ratcliffe 2004; Magrath, Haff, Horn, & Leonard 2010; Haff & Magrath 2011). For example, if sound waves travelling through nest walls are reduced in volume and bandwidth or increased in frequency, they should be less detectable or localizable by predators (reviewed in Magrath et al. 2010). However, sound waves may be reflected and redirected in cavity nests resulting in more directional, but potentially more detectable sounds emanating from the nest entrance (Mennill & Ratcliffe 2004). Whether enclosed nests, woven together with softer materials such as grasses or moss, have similar acoustic properties to wooden tree cavities is unclear (Potvin 2019). Dense vegetation or other habitat structure surrounding nests may also influence the visibility of nests (Martin 1992) and the transmission of begging noises, thereby reducing the importance of nest structure's effect on predation rates (Magrath et al. 2010). Tests of these alternatives to the common assumption that enclosed nests reduce offspring predation rates are lacking.

Here, we provide a test of these alternatives using experiments and long term observational data from a community of mid-elevation tropical songbirds. First, we tested whether enclosed nests are larger than open nests for a given body size and examined how nest structure and nest size influence nest predation rates across species. Second, we measured the acoustic properties of open and enclosed nests to determine how nest structure influences the detectability of sounds emanating from nests. We compared nest acoustics recorded in the field to those recorded in controlled lab environments to examine the effect of nest structure independent of the vegetation around nest sites. Next, we experimentally broadcast begging calls from *in situ* (inactive) nests to test the relative importance of visual and auditory cues for predation rates in open vs. enclosed nests. Finally, we compared stage-specific nest predation rates across species with open vs. enclosed nests to test whether increased auditory cues from begging nestlings influence nest predation rates compared with the lack of sound during incubation.

Materials and Methods:

Study Area, Species, and Nest Data:

We found 5503 nests of 30 songbird species (Table S1 in Supporting Information) in a mid-elevation (1450-1950m) tropical forest in Kinabalu Park, Sabah, Malaysia (6.2074° N, 116.6409° E) from 2009 to 2018. The nest predator community at this site is tremendously diverse, but two of the most common nest predators, the Short-tailed Magpie (*Cissa jefferyi*) and the Mountain Treeshrew (*Tupaia montana*) use both visual and auditory cues to find nests (pers. obs.; Heffner 2004). We categorized nests as enclosed when the nest cup was covered with constructed walls and a roof and open when the nest cup was not surrounded by constructed walls or a roof. We monitored all nests every 1-4 days to determine whether nests were depredated and stage transitions (Martin & Geupel 1993). We measured the outside diameter and height of 1061 nests during the incubation stage and estimated nest surface area assuming open cup nests were half of an ellipsoid while enclosed nests were a full ellipsoid (Fig. S1). Surface area is a good metric for nest size because it approximates the portion of the nest that is visible to predators (Biancucci & Martin 2010).

We captured and banded between 2 and 1297 adult birds of each species using mist nets and measured their mass using GemPro 250 portable electronic scales (MyWeigh, Phoneix, AZ, USA) with an accuracy of ±0.001g. Average mass was calculated for each species.

Nest Acoustics:

In 2018, we broadcast white noise (Fig. S2) from a small speaker (Groove Cube by WowWee Group Limited, Hong Kong) from inside recently used open and enclosed nests and made recordings to examine the effect of nest structure on the detectability of sound emanating from the nest. We recorded the sound with the speaker from four sides and directly overhead using a digital recorder (PMD 661 by Marantz, Chatsworth, CA, USA) and shotgun microphone (ME67 by Sennheiser, Old Lyme, CT, USA) located 67cm away from the speaker. We used the same audio track and playback equipment for each recording and always placed the speaker facing directly up. We ensured all settings on the speaker and recorder (e.g. gain) were identical for each recording. We recorded sound for *in situ* nests in the field (63 nests from 7 open cup nesting species and 6 enclosed nesting species). We also recorded sound for nests inside the laboratory (83 nests from 17 open cup nesting species and 8 enclosed nesting species) to control for the effects of vegetation and ambient conditions at the nest site. If an open cup nest only had one side that was accessible by parents due to vegetation or other aspects of nest site placement, we considered that side the front of the nest. Otherwise, we chose a side at random to be the front. We recorded the speaker playing white noise for at least 10 seconds for each side as well as an unobstructed control from outside the nest in a single continuous recording for each nest. We obtained measures of average power, center frequency, and 90% bandwidth (hereafter volume, frequency, and bandwidth) from each direction using Raven Pro (Bioacoustics Research Program 2014). High volume and low frequency sound waves travel further because they are less likely to be absorbed or scattered by the atmosphere or by objects in their path (Wiley & Richards 1982; Magrath et al. 2010). Higher bandwidth calls are generally more localizable due to differences in the attenuation between high and low frequencies (Magrath et al. 2010). Since there was substantial background noise between 0-200Hz and this band of frequencies was well below the frequencies produced by the playback, we removed sound at these frequencies from all recordings. Raven only provides relative measures of power within recordings, so we subtracted power values for nest measurements from control measurements for each nest.

Predation Experiment:

In 2018, we collected recently used nests from two species: Bornean Whistler (*Pachycephala hypoxantha*; open nest) and White-browed Shortwing (*Brachypteryx montana*; enclosed nest) to test the effect of nest structure on predation rates. For each replicate (n=26), we placed four nests (two from each species) 30-50m apart from one another with one quail egg and one white plasticine egg (about 2cm in length) inside the nest. We placed all nests in sites surrounded by similar density of vegetation and between 0.5-1.5m above the ground that would be reasonable sites for both species. Because empty, recently used nests for these two species were limited, we reused some nests between replicates but alternated the treatment they were assigned. For one nest of each species we used a small speaker (Groove Cube by WowWee Group Limited, Hong Kong) to broadcast begging recordings. Each speaker was attached to an mp3 player (Sansa Clip by SanDisk, Milpitas, CA, USA) playing a continuous track containing 10 seconds of begging vocalizations followed by 50 seconds of silence. This pattern of playback simulated the short and repeated bouts of begging that occur when parents come to the nest to feed. Peak amplitude of all begging recordings peaked between 50-60 dB as recorded by a sound level meter at 15cm without obstructions (Model 407730, Extech Instruments Corporation, USA). The mp3 player was kept inside a waterproof bag and both the bag and the speaker were camouflaged. Previous studies have shown that species' begging calls may be adapted to the nest structure they experience (Haskell 2002). This made it problematic to use begging recordings from the species which built each experimental nest type because the intrinsic acoustic properties of the nest structure could be confounded with differences in begging call structure. Thus, we used begging recordings from a third species (Mountain Wren-babbler; *Napothera crassa*) which builds a nest that is intermediate in structure between the two experimental nest types. Five unique begging recordings from different nests were used. Speakers were set up within 1 hour of sunrise and left to broadcast for approximately 8 hours. One nest of each species did not have speakers playing at them, but had identical wires and bags set up each day. The contents of each nest were scored as depredated or not depredated after 10 days. We considered any missing eggs, broken quail eggs, fresh marks in the plasticine eggs, or destroyed nests as signs of predation.

Statistical Analyses:

We used phylogenetic generalized least squares (PGLS) models to test if (1) enclosed nests are larger than open cup nests and if (2) mean nest predation rates increased with nest size. Larger species have larger nests (Biancucci & Martin 2010), so we included adult body size as a covariate to account for its effect on nest size independent of nest structure. Larger nests also experience lower nest predation rates (T.E.M. unpublished data) due to the fact that small predators often are most common and may be less able to depredate larger offspring (e.g. DeGraaf & Maier 1996) or because larger parents can more easily deter nearby predators (Montgomerie & Weatherhead 1988). Thus, we also included adult body size as a covariate to account for its effect on nest predation independent of nest size. Mean nest predation rates were calculated using the Mayfield method (Mayfield 1961) to account for exposure time for 26 species with adequate sample size. We obtained a distribution of 1000 trees from birdtree.org (Jetz, Thomas, Joy, Hartmann, & Mooers 2012) using the Hackett et al. (2008) backbone and created a majority-rules consensus tree in program Mesquite (Maddison & Maddison 2011). This tree was then used in the model to account for possible phylogenetic effects. We log transformed adult body mass and nest size to meet model assumptions.

We used linear mixed effect models to examine how nest structure influences the volume, bandwidth, and frequency of sounds emanating from inside the nest. We included an interaction between nest structure and the direction of each recording (front, side, rear, or top) and nested random effects for each individual nest within species. We ran separate models for lab and field recordings. We tested for pairwise differences between nest types for each recording direction using estimated marginal means. We corrected for multiple comparisons using the Tukey method.

We used a logistic mixed effects model to examine how nest structure and broadcast begging calls interact to influence the probability of nest predation in experimental nests. We included nest type, begging treatment, and their interaction as fixed effects. We accounted for variation in ambient risk between replicates using random effects. We tested for pairwise differences between all combinations of nest type and begging treatment using estimated marginal means.

We used phylogenetic generalized least squares models to examine stage-specific predation rates. We tested whether nest structure influenced nest predation rates during the incubation and nestling stages after controlling for adult body mass. We also tested whether nest structure affected the difference in predation rates between nestling and incubation stages. We used the same phylogenetic tree described for the nest size analyses above.

Results:

Nest Size:

Nest size increased with adult body mass across species and enclosed nests were larger than open nests for a given body mass (Fig. 1a; Table 1a). Mean nest predation rates decreased with adult body mass (Fig. 1b). After accounting for body size, nest predation rates increased with nest size, but did not differ between open vs. enclosed nests across species (Fig. 1b-c; Table 1b).

Nest Acoustics:

The effect of nest structure on the detectability of sounds broadcast from the nest differed between lab and field tests, the acoustic metric considered, and the direction of the recording in relation to the nest (Fig. 2; Table S2-3). In the lab, sounds were louder with higher bandwidth from enclosed nests than open cup nests when recorded from the front, but were quieter and lower bandwidth when measured from the rear and the top (Fig. 2a, b). However, the frequency of the sound was lower from enclosed nests than open cup nests in every direction except the front (Fig. 2c). In the field, sounds emanating from enclosed nests were marginally louder when measured from the top (Fig. 2d), had lower bandwidth when measured from the side or top (Fig. 2e) and, were lower frequency from all directions except the rear (Fig. 2f).

Predation Experiment:

The effect of nest type on nest predation rates among experimental nests varied depending on begging playback treatment (Fig. 3a; Table 2). Enclosed nests without begging playback experienced marginally less predation than open nests without begging playback, but did not differ from open nests with begging playback. Begging playback increased predation rates for enclosed nests, but did not influence predation among open cup nests. Enclosed nests with begging playback experienced similar levels of predation as open nests with or without begging playback.

Stage-Specific Nest Predation:

Nest type did not explain variation in mean nest predation rates during either the incubation (Table 3a) or nestling stage (Table 3b) among natural nests. However, nest predation increased between the incubation and nestling stages in enclosed but not open nests (Fig. 3b; Table 3c).

Discussion:

Mitigating offspring predation risk is thought to be one of the major functions of animal nests. Enclosed nests in particular are thought to provide increased nest predation benefits compared to open nests (Wallace 1889; Nice 1957; Oniki 1985). This idea is widespread and has been used as the basis for phylogenetic studies examining the evolution of nest structure (e.g. Hall et al. 2015). Yet, despite the importance of selection from nest predation and the fact that enclosed nests are ancestral among songbirds, open nests are more common (Martin et al. 2017; Price & Griffith 2017; Fang et al. 2018). Here, we provide evidence that (1) enclosed nests are more detectable to nest predators because they are relatively larger for a given body size and (2) enclosed nests do not consistently reduce the detectability of auditory cues compared to open cup nests as commonly assumed.

Enclosed nests are expected to buffer any noises coming from inside and thereby reduce the detectability of nests due to auditory cues (Lampe et al. 2004; Magrath et al. 2010). Indeed, we found the bandwidth of sounds emanating from enclosed nests was often reduced compared to open nests in both the lab and field which is thought to reduce their detectability by predators (Fig. 2; Magrath et al. 2010). The volume of sound was also reduced by enclosed relative to open nests from the rear and top of nests in the lab, but not the field. Yet, increased auditory cues were associated with greater increases in predation in enclosed than open nests in both our experimental (Fig. 3a; Table 2) and natural nests (Fig. 3b; Table 3). These results may reflect our finding that sounds were louder with greater bandwidth from the front of enclosed nests than open nests which is thought to increase their detectability by predators (Fig. 2; Magrath et al. 2010). Interestingly, we detected this effect when we analyzed recordings made in the lab and not in the field. Vegetation, background noise and physical terrain around nest sites may have a major influence on the acoustic properties of natural nests. Yet, even in the field, sounds were often lower frequency and even marginally higher volume from one direction in enclosed compared to open nests (Fig. 3d, f). Enclosed nests also reduced the frequency of begging calls from most sides both in the field and lab which is thought to increase detectability by predators (Fig. 2; Magrath et al. 2010). This pattern is likely due in part to filtering of high frequency sounds in enclosed but not open nests which may not have a strong influence on detection by predators if associated with quieter noises overall. Still, volume was similar or marginally increased in enclosed compared with open nests from two directions (Fig. 2). Acoustic properties of nests may also be similarly important in other taxa. For example, the vocalizations of many rodent pups can be used by predators to find nests (Arch & Narins 2008; Ylönen, Kasi, Opperbeck, Haapakoski, & Sundell 2017) and nest structure may influence the detectability of these noises, though tests of this idea in other taxa are lacking.

Enclosed nests are also thought to decrease predation risk because their roof and walls can obscure sight of conspicuous eggs and nestlings by visually searching predators (Wallace 1889; Collias & Collias 1984). In support of this idea, enclosed nests suffered marginally less predation than open cup nests in our predation experiment when no begging sounds were broadcast (Fig. 3; Table 2). However, we did not find any difference in predation rates between nest types during the incubation stage in natural nests in this system when no begging cues were present (Fig. 3b). This discrepancy between experimental and comparative results could reflect some limitations of artificial nest experiments. We included plasticine eggs in our experiment to ensure we detected small predators that would be unable to break through the shell of quail eggs (Roper 1992). However, plasticine eggs have a smell that may increase detection by predators that focus on olfactory cues (Rangen, Clark, & Hobson 2000). If enclosed nests limit the spread of these olfactory cues relative to open nests by blocking airflow over the nest contents, enclosed nests without begging playback might experience reduced predation. Future studies could address this issue by replicating this experiment with smaller eggs such as finch eggs that would not exclude smaller predators but provide no additional olfactory cues. Furthermore, our experiment only used nests from two species while the comparative data come from a much broader range of species. Nonetheless, our experiment and stage-specific comparative data show similar qualitative patterns (Fig. 3) suggesting that enclosed nests do not provide major predation benefits over open nests.

The sensory biases of predators in a given community may influence the detectability of nests and the importance of different functional properties of nest structures. For example, in communities consisting predominantly of visually oriented predators, the acoustic properties of nests may have little influence on offspring predation rates. The nest predator community in Borneo montane forest is highly diverse with many known or likely avian, mammalian and reptilian predators. The most common nest predators, Short-tailed Magpie (*Cissa jefferyi*) and Mountain Treeshrew (*Tupaia montana*), rely on both visual and auditory cues in the frequency range of begging calls to find nests (pers. obs.; Heffner 2004). Thus, both the visual and acoustic properties of nests should influence nest predation rates at our site. However, the effect of nest structure on predation rates may differ in other ecosystems with less diverse predator communities and more distinct sensory biases.

Our results suggest that enclosed nesting songbird species may not be any less sensitive to changes in predation pressure than open nesting species. Life history traits (LaManna & Martin 2016) or evolved nest site preferences (Martin 1992; Lampila, Monkkonen, & Desrochers 2005; LaManna, Hemenway, Boccadori, & Martin 2015) that influence susceptibility to predation risk may be more important for linking nest predation risk to population dynamics. Additionally, enclosed nests may not relax selection by predation risk on parental care traits such as offspring provisioning or nest attentiveness compared to open nests. Instead, enclosed nests may provide benefits by mitigating effects of abiotic factors such as temperature and precipitation on offspring or adults (Mainwaring, Hartley, Lambrechts, & Deeming 2014; Martin et al. 2017). Thus, nest structure could be important for predicting how populations will respond to changing abiotic conditions (Nelson, Thompson, Pledger, Keall, & Daugherty 2004; Peoples, Tainer, & Frimpong 2011).

By taking a functional and experimental approach towards studying the influence of nest structure on offspring predation rates, we show that enclosed nests are not necessarily less detectable by predators compared to open nests in contrast to long held views. For a given body size, enclosed nests are larger than open cup nests which can make them more detectable to visually oriented predators. Furthermore, enclosed nests do not reduce the detectability of begging calls by predators compared to open nests. Together, these findings help explain why enclosed nests are not more common among songbirds. Other functions, such as protecting young from sun, rain, wind, and severe air temperatures may play a stronger role than currently recognized. The relative importance of nest size, location, and structure may vary in other taxa with diverse natural histories (e.g. in species without conspicuous begging displays). Additional comparative and functional analyses promise to improve our understanding of the role of nest structure in shaping ecology and evolution in natural systems.

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References:

Arch, V.S., & Narins, P.M. (2008). “Silent” signals: Selective forces acting on ultrasonic communication systems in terrestrial vertebrates. Animal Behaviour, 76, 1423-1428.

Biancucci, L., & Martin, T.E. (2010). Can selection on nest size from nest predation explain the latitudinal gradient in clutch size? Journal of Animal Ecology, 79, 1086–1092.

Bioacoustics Research Program. (2014). Raven Pro: Interactive Sound Analysis Software (Version 1.5) [Computer software]. Ithaca, NY: The Cornell Lab of Ornithology. http://www.birds.cornell.edu/raven.

Briskie, J.V., Martin, P.R., & Martin, T.E. (1999). Nest predation and the evolution of nestling begging calls. Proceedings of the Royal Society of London B: Biological Sciences, 266, 2153-2159.

Collias, N. E. (1997). On the origin and evolution of nest building by passerine birds. Condor, 99, 253–270.

Collias, N.E., & Collias, E.C. (1984). Nest building and bird behavior. Princeton University Press, Princeton, NJ, USA.

DeGraaf, R.M. & Maier, T.J. (1996). Effect of egg size on predation by white-footed mice. Wilson Bulletin, 108, 535-539.

Eckert, G. J. (1987). Estimates of adult and juvenile mortality for labrid fishes at One Tree Reef, Great Barrier Reef. Marine Biology, 95, 167-171.

Fang, Y., Tuanmu, M., & Hung, C. (2018). Asynchronous evolution of interdependent nest characters across the avian phylogeny. Nature Communications, 9, 1863.

Gosselin, L. A., & Qian, P. Y. (1997). Juvenile mortality in benthic marine invertebrates. Marine Ecology Progress Series, 146, 265-282.

Hackett, S.J., Kimball, R.T., Reddy, S., Bowie, R.C., Braun, E.L., Braun, M.J., … Yuri, T. (2008). A phylogenomic study of birds reveals their evolutionary history. Science, 320, 1763-1768.

Haff, T.M., & Magrath, R.D. (2011). Calling at a cost: elevated nestling calling attracts predators to active nests. Biology Letters, 7, 493-495.

Hall, Z.J., Street, S.E., Auty, S., & Healy, S.D. (2015). The coevolution of building nests on the ground and domed nests in Timaliidae. Auk, 132, 584-593.

Haskell, D.G. (1994). Experimental evidence that nestling begging behavior incurs a cost due to nest predation. Proceedings of the Royal Society of London B: Biological Sciences, 257, 161-164.

Haskell, D.G. (2002). Begging behavior and nest predation. In J. Wright & M. L. Leonard (Eds.), *The Evolution of Begging* (pp. 163-172). Dordrecht, The Netherlands: Kluwer Academic Publishers.

Heffner, R. S. (2004). Primate hearing from a mammalian perspective. The Anatomical Record Part A, 281A, 1111-1122.

Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K., & Mooers, A. O. (2012). The global diversity of birds in space and time. Nature, 491, 444-448.

LaManna, J.A., & Martin T.E. (2016). Costs of fear: behavioral and life-history responses to risk and their demographic consequences vary across species. Ecology Letters, 19, 403-413.

LaManna, J.A., Hemenway, A.B., Boccadori, V., & Martin, T.E. (2015). Bird species turnover is related to changing predation risk along a vegetation gradient. Ecology, 96, 1670-1680.

Lampe, H.M., Dabelsteen, T., Larsen, O.N., & Pedersen, S.B. (2004). Degradation of song in a species using nesting holes: the Pied Flycatcher *Ficedula hypoleuca*. Anais da Academia Brasileira de Ciências, 76, 262-266.

Lampila, P., Monkkonen, M., & Desrochers, A. (2005). Demographic responses by birds to forest fragmentation. Conservation Biology, 19, 1537-1546.

Leech, S.M., & Leonard, M.L. (1997). Begging and the risk of predation in nestling birds. Behavioral Ecology, 8, 644-646.

Loiselle, B.A., & Hoppes, W.G. (1983). Nest predation in insular and mainland lowland rainforest in Panama. Condor, 85, 93-95.

Maddison, W. P., & Maddison, D. R. (2011). Mesquite: A modular system for evolutionary analysis. Version 2.75. http://mesquiteproject.org.

Magrath, R. D., Haff, T.M, Horn, A.G., & Leonard, M.L. (2010). Calling in the face of danger: predation risk and acoustic communication by parent birds and their offspring. Advances in the Study of Behavior, 41, 187-251.

Mainwaring, M.C., Hartley, I.R., Lambrechts, M.M., & Deeming, C.D. (2014). The design and function of birds' nests. Ecology and Evolution., 4, 3909-3928.

Mainwaring, M.C., Reynolds, S.J., & Weidinger, K. (2015). The influence of predation on the location and design of nests. In D. C. Deeming & S. J. Reynolds (Eds.), *Nests, Eggs, & Incubation* (pp. 50-64). Oxford, UK: Oxford University Press.

Manicom C., Schwarzkopf, L., Alford, R.A., & Schoener, T.W. (2008). Self-made shelters protect spiders from predation. Proceedings of the National Academy of Sciences of the United States of America, 105, 14903-14907.

Martin, T.E. (1992). Breeding productivity considerations: What are the appropriate habitat features for management? In J.M. Hagan & D.W. Johnston (Eds.), *Ecology and Conservation of Neotropical Migrants* (pp. 455-473). Washington DC, USA: Smithsonian Institution Press.

Martin, T. E., & Geupel, G. R. (1993). Nest-monitoring plots: Methods for locating nests and monitoring success. Journal of Field Ornithology, 64, 507-519.

Martin, T.E., Boyce, A.J., Fierro-Calderon, K., Mitchell, A.E., Armstad, C.E., Mouton, J.C., & Bin Soudi, E.E. (2017). Enclosed nests may provide greater thermal than nest predation benefits compared with open nests across latitudes. Functional Ecology, 31, 1231-1240.

Mayfield, H. (1961). Nest success calculated from exposure. Wilson Bulletin, 73, 255-261.

Mennill, D.J., & Ratcliffe, L.M. (2004). Nest cavity orientation in black-capped chickadees *Poecile atricapillus*: do the acoustic properties of cavities influence sound reception in the nest and extra-pair matings? Journal of Avian Biology, 35, 477-482.

Møller, A.P. (1989). Nest site selection across field-woodland ecotones: the effect of nest predation. Oikos, 56, 240-246.

Møller, A.P. (1990). Nest predation selects for small nest size in the blackbird. Oikos, 57, 237-240.

Montgomerie, R.D. & Weatherhead, P.J. (1988). Risks and rewards of nest defence by parent birds. The Quarterly Review of Biology, 63, 167-187.

Mouton, J.C. & Martin, T.E. (2019) Data from: Nest structure affects auditory and visual detectability, but not predation risk, in a tropical songbird community. Dryad Digital Repository. http://doi:10.5061/dryad.9cr73f9

Muchai, M., & du Plessis, M.A. (2005). Nest predation of grassland bird species increases with parental activity at the nest. Journal of Avian Biology, 36, 110-116.

Nelson, N.J., Thompson, M.B., Pledger, S., Keall, S.N., & Daugherty, C.H. (2004). Do TSD, sex ratios, and nest characteristics influence the vulnerability of tuatara to global warming? International Congress Series, 1275, 250-257.

Nice, M.M. (1957). Nesting success in altricial birds. Auk., 74, 305-321.

Oniki, Y. (1985). Why robin eggs are blue and birds build nests: statistical test for Amazonian birds. Ornithological Monographs, 36, 536-545.

Orizaola, G., & Braña, F. (2003). Oviposition behavior and vulnerability of eggs to predation in four newt species (genus *Triturus*). Herpetological Journal, 13, 121-124.

Peoples, B.K., Tainer, M.B., & Frimpong, E.A. (2011). Bluehead chub nesting activity: a potential mechanism of population persistence in degraded stream habitats. Environmental Biology of Fishes, 90, 379-391.

Potvin, D. A. (2019). Mud acts as a noise dampener in Australian passerine nests. Emu, 119, 45-52.

Price, J.J., & Griffith, S.C. (2017). Open cup nests evolved from roofed nests in early passerines. Proceedings of the Royal Society of London B: Biological Sciences, 284, 20162708.

Promislow, D. E., & Harvey, P. H. (1990). Living fast and dying young: A comparative analysis of life-history variation among mammals. Journal of Zoology, 220, 417-437.

Rand, A.S., & Dugan, B. (1983). Structure of complex iguana nests. Copeia, 3, 705-711.

Rangen, S.A., Clark, R.G., & Hobson, K.A. (2000). Visual and olfactory attributes of artificial nests. Auk, 117, 136-146.

Roper, J.J. (1992). Nest predation experiments with quail eggs: too much to swallow? Oikos, 65, 528-530.

Snow, D.W. (1978). The nest as a factor determining clutch-size in tropical birds. Journal of Ornithology., 119, 227-230.

Wallace, A.R. (1889). Darwinism. Project Gutenberg, Urbana, IL, USA, pp. 133-134.

Wiley, R. H., & Richards, D. G. (1982). Adaptations for acoustic communication in birds: sound transmission and signal detection. In D.E. Kroodsma & E.H. Miller (Eds.), *Acoustic communication in birds* (pp. 131-181). New York, NY, USA: Academic Press.

Ylönen, H., Kasi, M., Opperbeck, A., Haapakoski, M., & Sundell, J. (2017). How Do Infanticidal Male Bank Voles (*Myodes glareolus*) Find the Nest with Pups? Ethology, 123, 105-112.

Tables:

Table 1. Variation in (a) nest size (n=27 species) and (b) mean nest predation rates (n=26 species) among songbird species using open versus enclosed nests. Nest type effects are in comparison to open nests. We show fixed effect coefficients and standard errors (*B* (*se*)), *z*-values, significance, and Pagel’s Lambda from phylogenetic generalized least squares model. Lambda values near 1 indicate strong phylogenetic signal in the residuals, while values near 0 indicate very weak phylogenetic signal.

a) Nest size (Lambda = 0.902)

Variable	B (se)	t	P-value
Enclosed (vs. Open)	2412.169 (493.901)	4.984	<0.001
Log Adult Mass	2449.855 (268.044)	9.139	<0.001

b) Mean nest predation rates (Lambda = 0.833)

Variable	B (se)	t	P-value
Enclosed (vs. Open)	-0.010 (0.006)	-1.639	0.115
Log Adult Mass	-0.019 (0.004)	-4.024	<0.001
Log Nest size	0.021 (0.007)	2.974	0.007

Table 2. Pairwise comparisons between nest type and begging playback treatments on nest predation risk in experimental nests. We show estimates and standard errors (*B* (*se*)), *z*-values, and significance adjusted using the Tukey method.

Contrast	B (se)	z	P-value
Enclosed Begging- Open Begging	0.984 (0.832)	1.183	0.637
Enclosed Begging- Enclosed None	2.811 (0.964)	2.916	0.018
Enclosed Begging- Open None	0.671 (0.830)	0.809	0.850
Open Begging – Enclosed None	1.826 (0.860)	2.122	0.146
Open Begging- Open None	-0.312 (0.793)	-0.394	0.979
Enclosed None- Open None	-2.139 (0.889)	-2.405	0.076

Table 3. Results from phylogenetic generalized least squares regression models explaining variation in (a) mean nest predation rates during the incubation stage, (b) the nestling stage, and (c) their difference (nestling rate – incubation rate) among 26 songbird species using open versus enclosed nests (nest type). Nest type effects are in comparison to open nests. We show Pagel's lambda, fixed effect coefficients and standard errors (*B* (*se*)), *z*-values, and significance for each model. Lambda values near 1 indicate strong phylogenetic signal in the residuals, while values near 0 indicate very weak phylogenetic signal

a) Log mean incubation predation rates (Lambda = 0.740)

Variable	B (se)	t	P-value
Enclosed (vs. Open)	-0.079 (0.167)	-0.477	0.632
Log Mass	-0.257 (0.091)	-2.812	0.009

b) Mean nestling predation rates (Lambda = 0.696)

Variable	B (se)	t	P-value
Enclosed (vs. Open)	0.011 (0.007)	1.626	0.117
Log Mass	-0.007 (0.003)	-1.925	0.066

c) Difference between nestling and incubation predation rates (Lambda = 0.06)

Variable	B (se)	t	P-value
Enclosed (vs. Open)	0.015 (0.007)	2.07	0.049

Figure Legends:

Figure 1. The effect of body mass and nest structure on nest size and predation rates. (a) Nest size as a function of adult body mass for 27 species of songbirds that build open (black circles) and enclosed (orange circles) nests. Partial residual plots showing the effect of (b) adult body mass (n = 26 species) and (c) nest size (n = 26 species) on mean nest predation rates across species controlling for phylogenetic effects.

Figure 2**.** Effects of nest type on the volume, bandwidth, and frequency of sounds broadcast from nests in the (a-c) lab and in the (d-f) field. All measurements are relative to the control recordings and the average measurement for open nests. Enclosed nests are depicted in orange and open nests are depicted in black. Points depict marginal means and error bars depict standard error. Significant differences between nest types for each recording direction are denoted as † ($p<0.1$), * ($p<0.05$), or ** ($p<0.01$).

Figure 3. Daily nest predation rates for (a) experimental nests with vs. without begging playback and (b) natural nests for 26 species during the incubation and nestling periods. Enclosed nests are depicted with orange and open nests are depicted in black. Error bars depict standard error.

Figures:

Fig. 1:

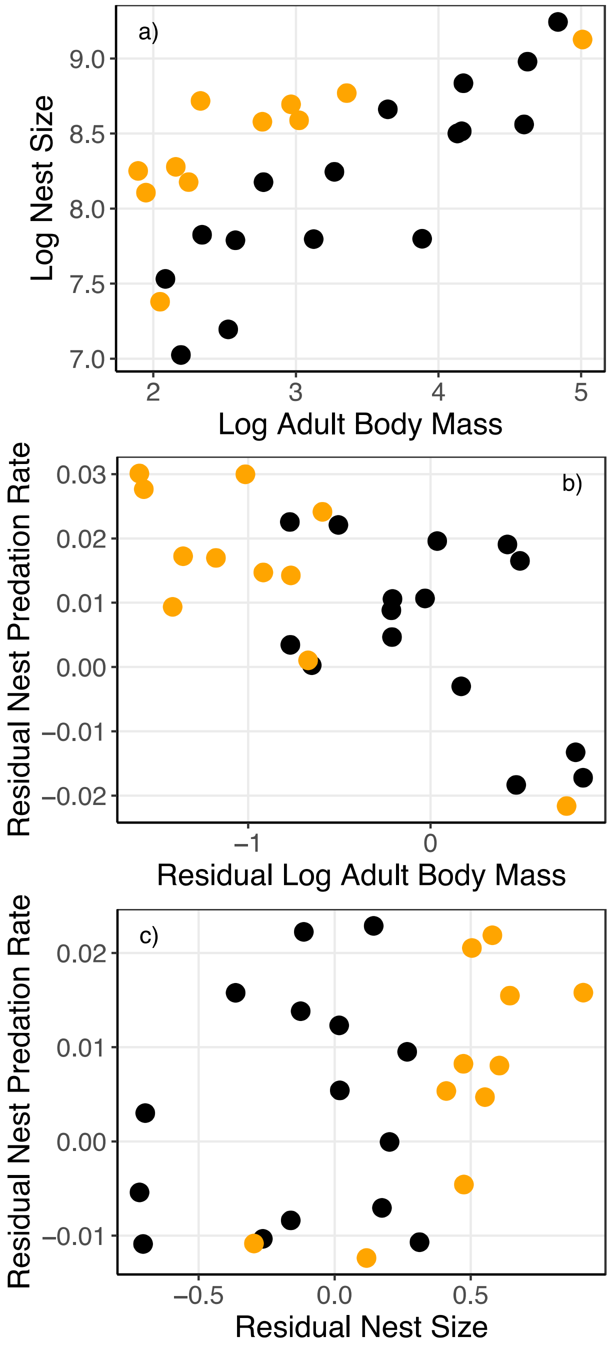
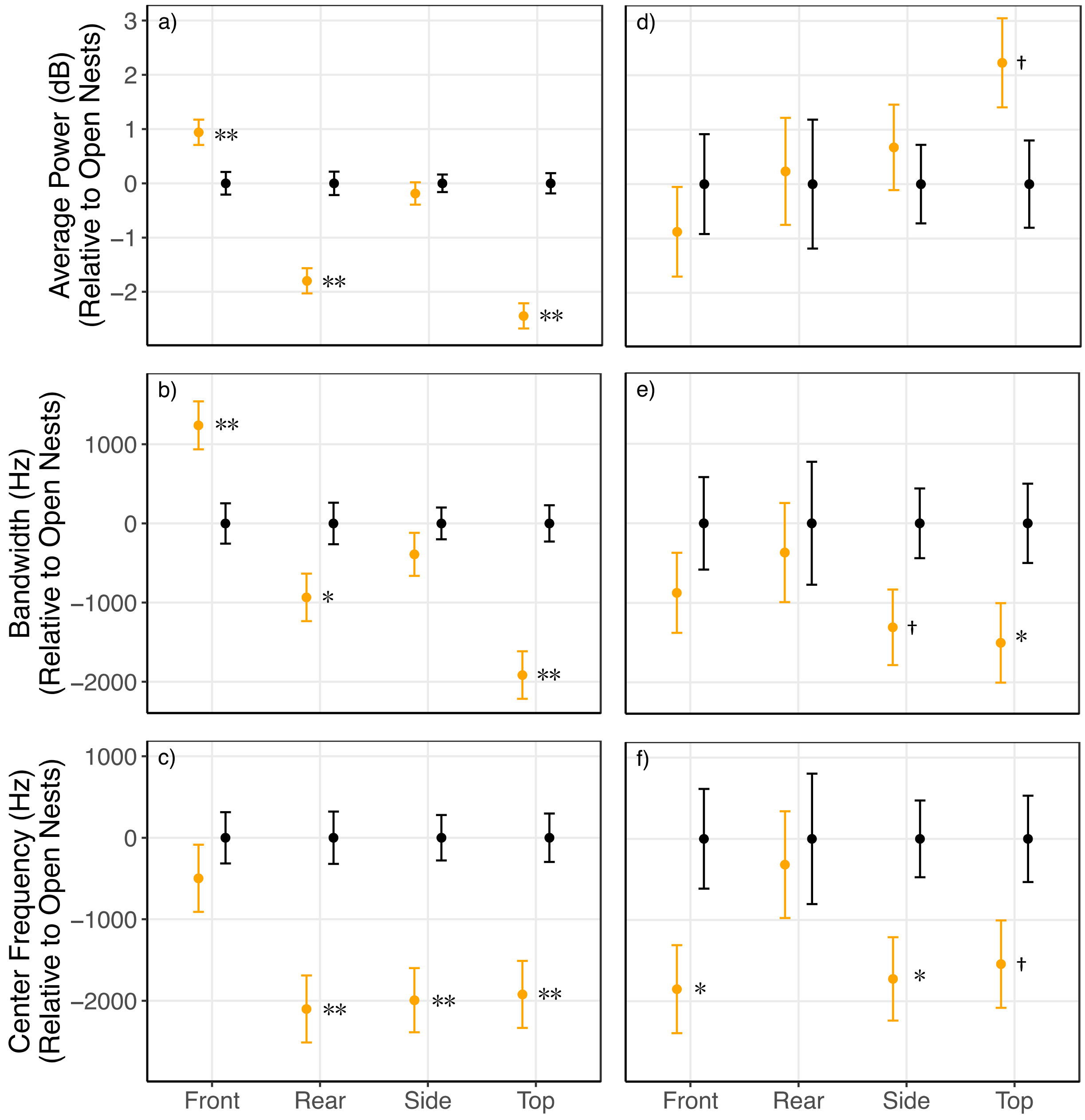


Fig. 2:


a)
b)
c)
d)
e)
f)
Average Power (dB)
(Relative to Open Nests)
Bandwidth (Hz)
(Relative to Open Nests)
Center Frequency (Hz)
(Relative to Open Nests)
3
2
1
0
−1
−2
1000
0
−1000
−2000
1000
0
−1000
−2000
**
**
**
**
*
**
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†
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*
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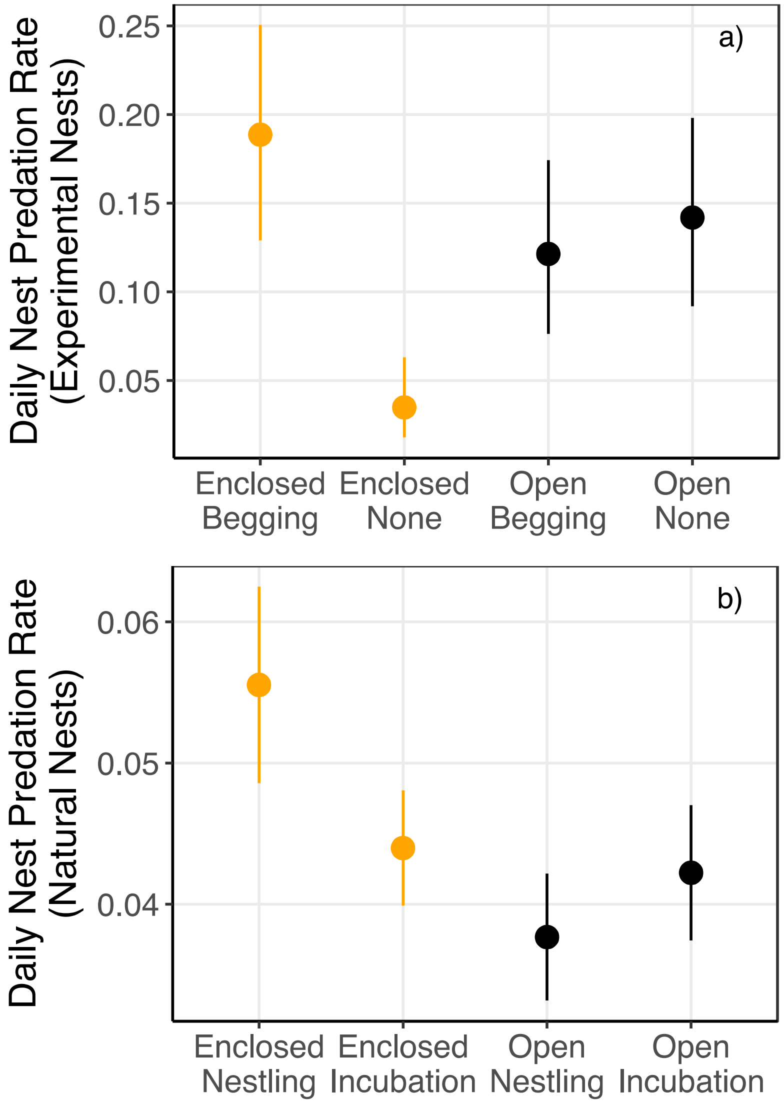
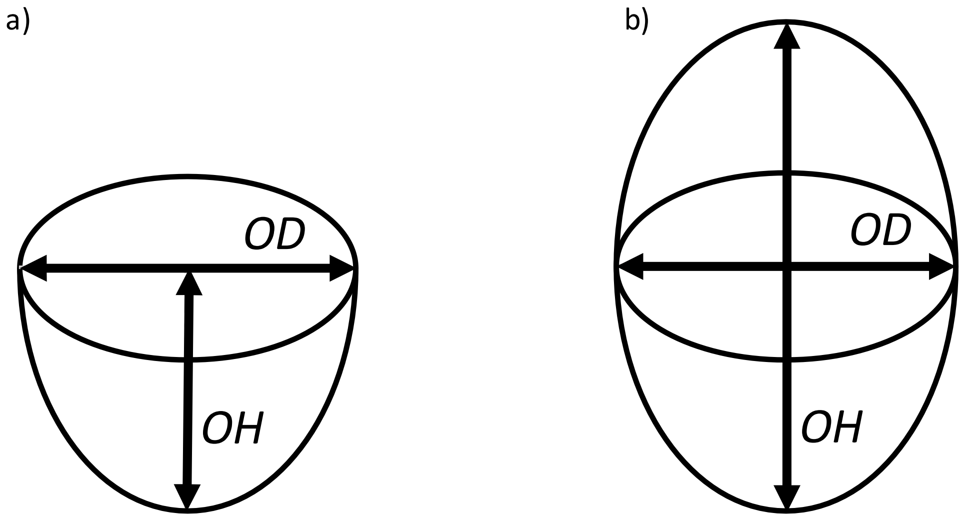
Front
Rear
Side
Top
Front
Rear
Side
Top

Fig. 3:


a)
Daily Nest Predation Rate
(Experimental Nests)
0.25
0.20
0.15
0.10
0.05
Enclosed
Begging
Enclosed
None
Open
Begging
Open
None
b)
Daily Nest Predation Rate
(Natural Nests)
0.06
0.05
0.04
Enclosed
Nestling
Enclosed
Incubation
Open
Nestling
Open
Incubation

Supporting Information:

Fig S1: Dimensions and equations for calculations of nest surface area (S) in (a) open and (b) enclosed nests. The outside diameter (OD) was measured from the outside edges of the nest through the center. The outside height (OH) was measured from the bottom nest to the tallest point of the nest from the outside. For open nests, we calculated surface area by adding half the surface are of an ellipse (i.e. the bottom of the nest) to the area of a circle forming the top of the nest. For enclosed nests, we calculated the surface area using the formula for the surface area of an ellipsoid. We include graphics of the measurements and show the formulas used



$$a = b = \frac{1}{2}OD \qquad c = OH$$

$$S = \frac{1}{2}4\pi\left(\frac{(ab)^{1.6}+(ac)^{1.6}+(bc)^{1.6}}{3}\right)^{1/1.6} + \pi b^2$$

$$a = b = \frac{1}{2}OD \qquad c = \frac{1}{2}OH$$

$$S = 4\pi\left(\frac{(ab)^{1.6}+(ac)^{1.6}+(bc)^{1.6}}{3}\right)^{1/1.6}$$

Fig. S2: A spectrogram of the white noise used to examine nest acoustics.

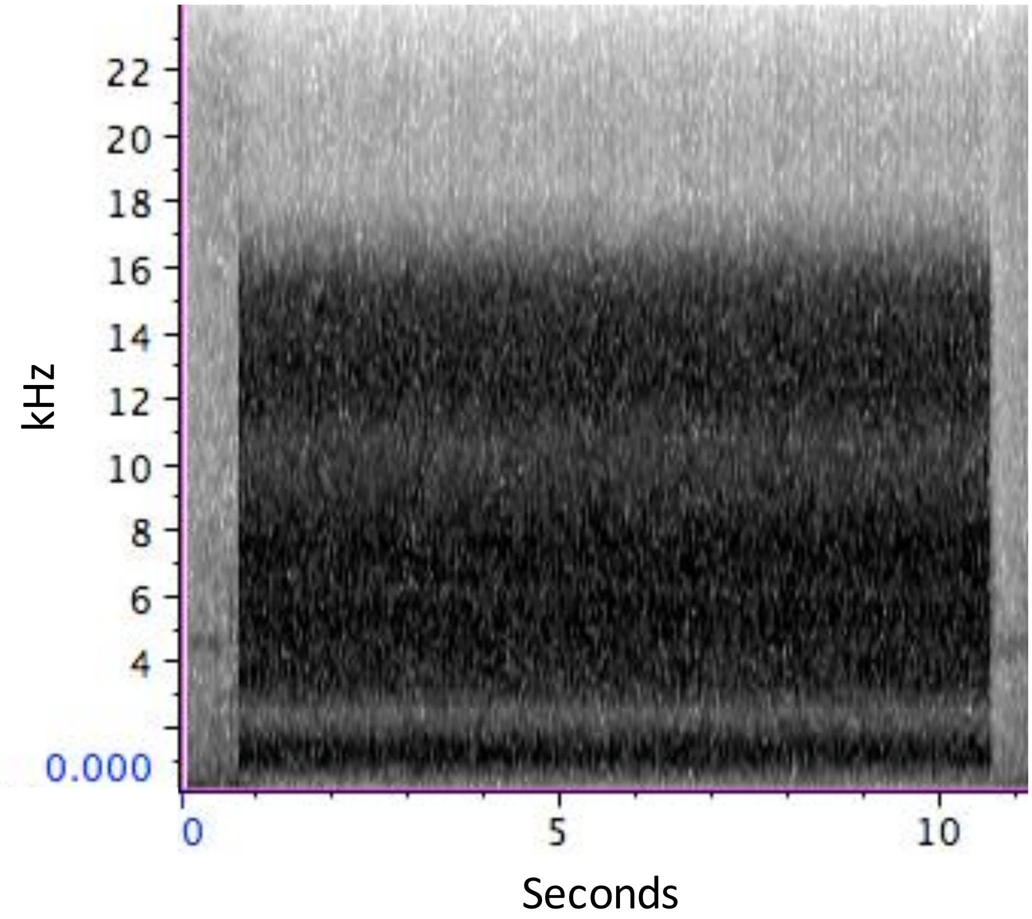


Table S1: Species list and samples sizes. NA indicates a species was not included in a particular analysis.

Common Names	Latin Name	Sample size					
		Nest Size (nests)	Body Size (indiv.)	Overall Predation Rate (nest/day)	Incubation Predation Rate (nest/day)	Nestling Predation Rate (nest/day)	Acoustics (lab/field)
Black-capped White-eye	*Zosterops atricapilla*	23	305	188 / 2080	147 / 1133	115 / 818	5 / 3
Bornean Forktail	*Enicurus leschenaulti*	33	77	73 / 920	54 / 532	41 / 350	2 / 0
Bornean Stubtail	*Urosphena whiteheadi*	58	106	108 / 1248	89 / 915	38 / 271	5 / 5
Bornean Treepie	*Dendrocitta occipitalis*	1	11	19 / 378	NA	16 / 202	1 / 0
Bornean Whistler	*Pachycephala hypoxantha*	79	348	365 / 4501	298 / 2953	174 / 1352	6 / 5
Bornean Whistling Thrush	*Myophonus borneensis*	21	53	116 / 2649	102 / 1293	72 / 1293	1 / 0
Chestnut-crested Yuhina	*Yuhina everetti*	236	524	771 / 8388	624 / 5215	344 / 2379	5 / 6
Chestnut-hooded Laughing Thrush	*Garrulax mitratus*	2	68	19 / 154	NA	NA	2 / 0
Eye-browed Jungle Flycatcher	*Rhinomyias gularis*	30	295	136 / 1767	107 / 1005	71 / 690	5 / 5
Fruithunter	*Chlamydochaera jefferyi*	4	2	49 / 844	38 / 404	31 / 407	1 / 0
Grey-throated Babbler	*Stachyris nigriceps*	91	1297	357 / 3522	260 / 2154	204 / 1102	5 / 5
Indigo Flycatcher	*Eumyias indigo*	21	26	120 / 1822	105 / 1113	60 / 624	2 / 0
Little Pied Flycatcher	*Ficedula westermanni*	9	11	52 / 653	37 / 388	25 / 231	NA
Mountain Leaf Warbler	*Phylloscopus trivirgatus*	33	156	160 / 2090	129 / 1383	81 / 571	6 / 5
Mountain Tailorbird	*Orthotomus cuculatus*	16	66	190 / 1990	121 / 1153	103 / 676	NA

Mountain Wren Babbler	*Napothera crassa*	43	153	132 / 1654	102 / 1180	55 / 393	4 / 6
Ochraceous Bulbul	*Alophoixus ochraceus*	6	168	41 / 520	25 / 244	32 / 266	6 / 3
Orange-headed Thrush	*Zoothera citrina*	1	26	NA	NA	NA	NA
Snowy-browed Flycatcher	*Ficedula hyperythra*	89	311	427 / 5138	353 / 3291	174 / 1576	3 / 4
Sunda Bush Warbler	*Cettia vulcania*	2	50	45 / 463	36 / 312	NA	1 / 0
Sunda Laughing Thrush	*Garrulax palliatus*	1	68	20 / 246	NA	NA	1 / 0
Temminck's Babbler	*Trichastoma pyrrogenys*	40	168	143 / 1766	110 / 1137	89 / 595	4 / 5
Temminck's Sunbird	*Aethopyga temminckii*	10	41	63 / 830	48 / 520	37 / 300	NA
White-browed Shortwing	*Brachypteryx montana*	70	91	308 / 4102	260 / 2471	133 / 1364	9 / 6
Whitehead's Broadbill	*Calyptomena whiteheadi*	1	6	30 / 762	23 / 347	22 / 397	1 / 0
White-throated Fantail	*Rhipidura albicollis*	90	262	230 / 2776	194 / 1723	107 / 917	5 / 5
Yellow-breasted Warbler	*Seicercus montis*	51	227	272 / 2386	178 / 1386	117 / 741	NA
Everett's Thrush	*Zoothera everetti*	NA	NA	NA	NA	NA	1 / 0
Hair-crested Drongo	*Dicrurus hottentottus*	NA	NA	NA	NA	NA	1 / 0
Island Thrush	*Turdus poliocephalus*	NA	NA	NA	NA	NA	1 / 0

Table S2: Nest acoustics recorded in the lab: Variation in (a) volume (average power), (b) bandwidth, and (c) frequency of sounds broadcast from nests explained by nest structure and direction of recording. We show fixed effect coefficients and standard errors (*B* (se)), t values, and significance from a linear mixed model. We controlled for differences among individual nests (n=83) and species (n=25) using nested random effects. Estimates show contrasts with an enclosed nest and recordings from the front.

a) Average Power:

Variable	B (se)	t	P-value
Open Nest	-0.940 (0.313)	-2.997	0.004
Rear	-2.682 (0.220)	-12.18	<0.001
Side	-0.894 (0.192)	-4.647	<0.001
Top	4.290 (0.220)	19.49	<0.001
Open Nest * Rear	2.727 (0.312)	8.776	<0.001
Open Nest * Side	1.127 (0.265)	4.253	<0.001
Open Nest * Top	3.385 (0.298)	11.355	<0.001

b) Bandwidth:

Variable	B (se)	t	P-value
Open Nest	-1238.93 (395.46)	-3.133	0.003
Rear	-1622.31 (264.75)	-6.335	<0.001
Side	-1386.64 (231.31)	-5.995	<0.001
Top	61.32 (264.75)	0.232	0.816
Open Nest * Rear	2172.51 (375.10)	5.792	<0.001

Open Nest * Side	1682.75 (318.14)	5.120	<0.001
Open Nest * Top	3153.26 (358.31)	8.800	<0.001

c) Center Frequency:

Variable	B (se)	t	P-value
Open Nest	497.38 (519.14)	0.958	0.345
Rear	-1375.14 (249.52)	-5.511	<0.001
Side	-1292.67 (217.98)	-5.930	<0.001
Top	1505.55 (249.52)	6.034	<0.001
Open Nest * Rear	1603.80 (353.52)	4.537	<0.001
Open Nest * Side	1496.20 (300.00)	4.987	<0.001
Open Nest * Top	1425.10 (337.78)	4.219	<0.001

Table S3: Nest acoustics recorded in the field: Variation in (a) volume (average power), (b) bandwidth, and (c) frequency of sounds broadcast from nests explained by nest structure and direction of recording. We show fixed effect coefficients and standard errors (*B* (se)), t values, and significance from a linear mixed model. We controlled for differences among individual nests (n=63) and species (n=13) using nested random effects. Estimates show contrasts with an enclosed nest and recordings from the front.

a) Average Power:

Variable	B (se)	t	P-value
Open Nest	0.877 (1.234)	0.711	0.484
Rear	-4.283 (0.822)	-5.206	<0.001
Side	-1.988 (0.567)	-3.505	<0.001
Top	1.951 (0.611)	3.192	0.001
Open Nest * Rear	-1.111 (1.424)	-0.780	0.436
Open Nest * Side	-1.552 (0.916)	-1.693	0.092
Open Nest * Top	-3.107 (0.994)	-3.125	0.002

b) Bandwidth:

Variable	B (se)	t	P-value
Open Nest	874.32 (768.77)	1.137	0.265
Rear	-1670.39 (558.20)	-2.992	0.003
Side	-1812.62 (383.72)	-4.724	<0.001
Top	-1123.64 (412.62)	-2.773	0.007
Open Nest * Rear	-507.05 (965.07)	-0.525	0.599

Open Nest * Side	433.69 (619.87)	0.700	0.485
Open Nest * Top	629.28 (183.17)	0.936	0.350

c) Center Frequency:

Variable	B (se)	t	P-value
Open Nest	1851.12 (818.51)	2.262	0.032
Rear	-890.10 (568.65)	-1.565	0.119
Side	-1105.26 (391.49)	-2.823	0.005
Top	218.88 (421.37)	0.519	0.604
Open Nest * Rear	-1533.63 (983.91)	-1.559	0.120
Open Nest * Side	-126.04 (632.49)	-0.199	0.842
Open Nest * Top	-308.71 (686.00)	-0.450	0.653

Table S4. Effects of nest type and begging playback on nest predation risk in experimental nests. Nest type effects are in comparison to open nests. We show fixed effect coefficients and standard errors (*B* (*se*)), *z*-values, and significance from a logistic mixed effect model.

Variable	B (se)	z	P-value
Enclosed (vs. Open)	-0.984 (0.832)	-1.183	0.236
Begging Playback	-2.811 (0.964)	-2.916	0.003
Enclosed * Begging Playback	3.124 (1.270)	2.460	0.013