

Seasonal fecundity and costs to λ are more strongly affected by direct than indirect predation effects across species

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Abstract. Increased perceived predation risk can cause behavioral and physiological responses to reduce direct predation mortality, but these responses can also cause demographic costs through reduced reproductive output. Such indirect costs of predation risk have received increased attention in recent years, but the relative importance of direct vs. indirect predation costs to population growth (λ) across species remains unclear. We measured direct nest predation rates as well as indirect benefits (i.e., reduced predation rates) and costs (i.e., decreased reproductive output) arising from parental responses to perceived offspring predation risk for 10 songbird species breeding along natural gradients in nest predation risk. We show that reductions in seasonal fecundity from behavioral responses to perceived predation risk represent significant demographic costs for six of the 10 species. However, demographic costs from these indirect predation effects on seasonal fecundity comprised only 12% of cumulative predation costs averaged across species. In contrast, costs from direct predation mortality comprised 88% of cumulative predation costs averaged across species. Demographic costs from direct offspring predation were relatively more important for species with higher within-season residual-reproductive value (i.e., multiple-brooded species) than for species with lower residual-reproductive value (i.e., single-brooded species). Costs from indirect predation effects were significant across single- but not multiple-brooded species. Ultimately, demographic costs from behavioral responses to offspring predation risk differed among species as a function of their life-history strategies. Yet direct predation mortality generally wielded a stronger influence than indirect effects on seasonal fecundity and projected λ across species.

Key words: demographic costs; fitness; indirect effects; landscape of fear; life-history; mortality; predation; predation risk; reproductive success; seasonal fecundity.

INTRODUCTION

Individuals of any given species are distributed across a “landscape of fear” (sensu Laundré et al. 2010) characterized by differences in predation risk. Variation in risk across the landscape is a powerful ecological force, determining rates of direct-predation mortality and demography, as well as shaping the distributions and abundances of species (Martin 1988, Robinson et al. 1995, Marchand and Litvaitis 2004, Creel and Christianson 2008, LaManna et al. 2015). Behavioral and morphological responses to increased predation risk can reduce the probability of direct predation mortality but also create additional indirect demographic costs that have been observed across taxa, including aquatic species (Lima and Dill 1990, Preisser et al. 2005), amphibians (Werner and Anholt 1996, Relyea and Werner 1999, Van Buskirk 2000), mammals (Creel et al. 2007), and birds (Fontaine and Martin 2006a, Zanette et al. 2011, Ibáñez-Álamo et al. 2015). For example, birds nesting in riskier habitat can reduce nest visits to prevent predators from locating

the nest, but this strategy can result in less food delivered to the nest, lower offspring quality, and even starvation of one or more offspring (Fontaine and Martin 2006a, Zanette et al. 2011). *Daphnia* can grow elongated crests and tails in the presence of chemical cues from their predators, but these morphological defenses are associated with reduced reproductive output (Barry 1994). Such indirect costs may decrease population growth rates beyond direct predation alone (Fig. 1a; Preisser et al. 2005, Creel and Christianson 2008), and the extent of costs appear to differ among species (compare 1–3 in Fig. 1a; Relyea 2001, Ghalambor et al. 2013, LaManna and Martin 2016). Yet, the reasons why the severity of these indirect costs differs among species remain unclear. A comparative study is needed to evaluate which factors determine the relative importance of direct and indirect predation costs to demography across species.

Direct predation mortality, by definition, increases with risk because risk is estimated by the probability of predation. Indirect predation costs may also increase with risk and may exceed direct predation costs across species (Fig. 1b; reviewed in Preisser et al. 2005). Of course, direct predation might have the larger influence on cumulative predation costs across species (Fig. 1c, d; Sih 1987, Lima and Dill 1990, Relyea 2001, Martin and

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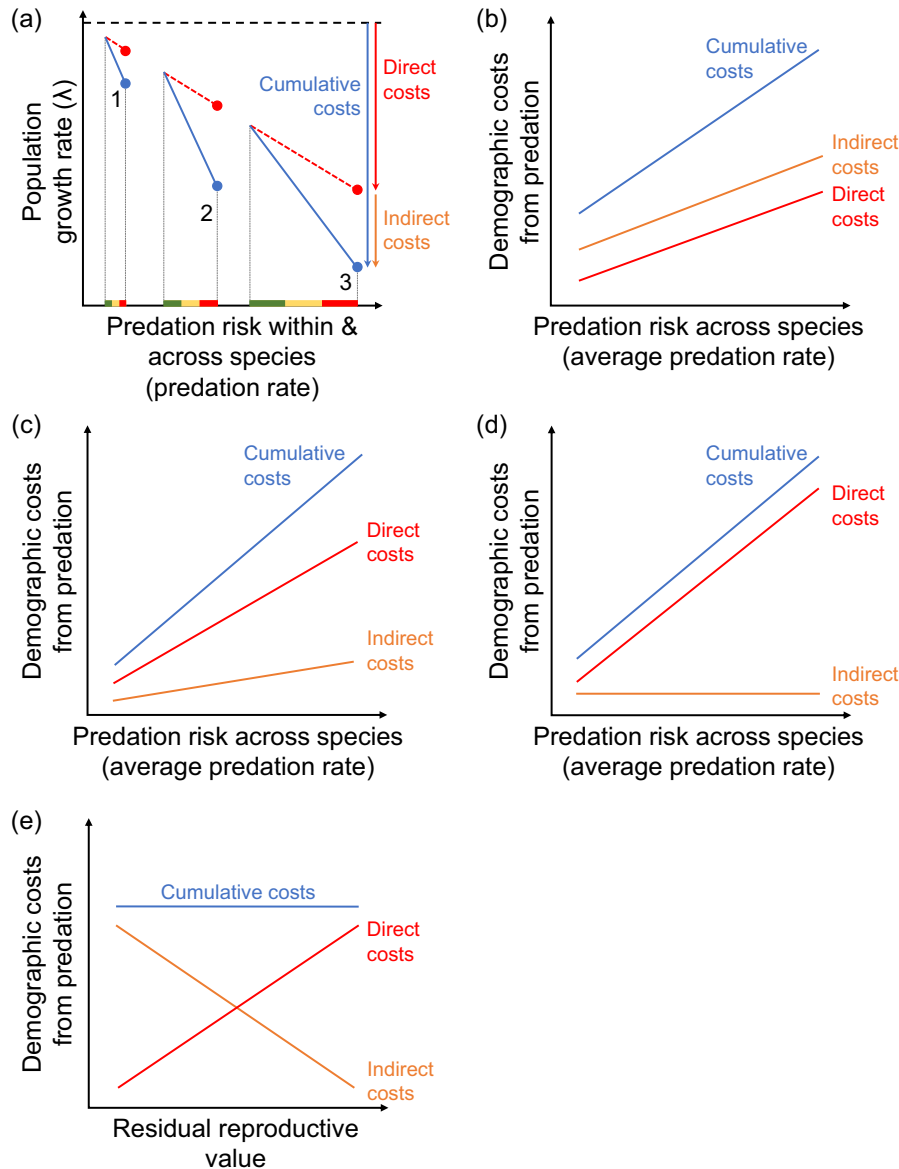


FIG. 1. Predation risk can vary for any species across a landscape of fear. High-risk habitats, red on x -axis in (a), have higher direct predation mortality than low-risk habitats, green on x -axis in (a). However, fewer young are produced in high-risk compared to low-risk habitat because of behavioral and physiological responses to increased risk (i.e., indirect-predation costs). (a) Within-species variation in population growth rate (λ) due to direct predation mortality and cumulative direct and indirect predation costs for three hypothetical species that differ in average predation rates. Naturally, direct predation mortality will have greater demographic costs (red) for species with higher average predation rates (species 3 compared to species 2 or 1). (b) Cumulative demographic costs from predation (direct plus indirect costs; blue) may increase with average predation rates across species if indirect costs (orange) are large but proportional to direct costs. Cumulative predation costs may still increase with average predation rates across species if indirect costs (c) increase at a slower rate than direct costs or (d) do not vary with risk at all, causing direct costs to represent an increasingly larger proportion of cumulative costs. In these cases (b–d), variation in direct predation costs among species will reflect the full selective force of predation on trait evolution and cumulative direct and indirect effects of predation on λ . (e) However, if indirect predation costs strongly influence demography and vary with other life-history traits (e.g., residual reproductive value), then variation in direct predation costs across species may be decoupled from variation in cumulative predation costs. In this case, variation in direct predation costs among species will not reflect the full selective force of predation on trait evolution nor the cumulative direct and indirect effects of predation on λ .

Briskie 2009, Ghalambor et al. 2013). Yet, indirect costs may increase at a slower rate than direct costs (Fig. 1c) or not vary with risk at all (Fig. 1d) across species,

causing direct costs to represent an increasingly larger proportion of cumulative costs. Any of these first alternatives (Fig. 1b–d) would lead to a correlation between

direct and cumulative predation costs, which is a critical assumption of many studies that use direct predation rates to index the relative influence of predation on demography or fitness (e.g., Martin 1995, Relyea 2001). Alternatively, life-history strategies might determine the severity of indirect predation costs among species, and indirect costs could potentially be greater for species with lower direct predation costs (Fig. 1e). For example, behavioral responses to increased perceived nest-predation risk differed among bird species as a function of their within-season residual-reproductive value (Clark 1994, LaManna and Martin 2016). Multiple-brooded species have a greater reproductive asset to protect within a breeding season, and respond to increased perceived risk in a way that mitigates indirect costs relative to single-brooded species (LaManna and Martin 2016). Yet multiple-brooded species generally have higher direct nest predation rates (i.e., direct predation costs) than single-brooded species (Martin 1995). Thus, multiple-brooded species likely have greater direct predation costs, but might have lower indirect-predation costs, than single-brooded species (Fig. 1e). If indirect costs from predation are affected by such life-history differences and are equal to or larger than direct costs, then indirect predation costs could have a relatively more important influence than direct predation costs on demography across species (Creel and Christianson 2008).

We used individual-based demographic models, which estimate population demographic rates using computer simulations of individual organisms (DeAngelis and Gross 1992, Lloyd et al. 2005), to assess the relative influence of direct and indirect predation costs on population seasonal fecundity, a critical component of demography and fitness (Pulliam 1988, 2000). We modeled seasonal fecundity for 10 songbird species that differed in average nest-predation rates and within-season residual-reproductive value (i.e., number of broods per season). We monitored nests, hence our assessment of predation effects pertains to the nesting period. This includes direct predation of offspring in nests as well as indirect costs and benefits resulting from responses of parental reproductive strategies (e.g., changes in clutch size, egg size, incubation activity, feeding visits) and nestling growth and development (e.g., reallocation of resources from body to wing or tarsus growth) to increased nest-predation risk. Daily nest-predation rates (i.e., direct costs) varied along habitat gradients (LaManna et al. 2015). Parent birds responded to increased nest-predation risk with behavioral responses that reduced the length of embryonic-development periods (Appendix S1: Fig. S1), which reduced the probability of time-dependent nest mortality and mitigated direct predation costs (LaManna and Martin 2016). However, increased predation risk was also associated with fewer offspring being produced in the absence of direct predation (Appendix S1: Fig. S1), representing an indirect cost of predation (LaManna and Martin 2016). While LaManna and Martin (2016) documented the existence

of these indirect predation effects based on both experimental and observational tests, they did not examine the relative importance nor cumulative impact of direct and indirect predation effects to seasonal fecundity and population growth rates (λ). Here, we parameterize individual-based demographic models with data collected over 6 yr to compare the relative importance of direct and indirect predation costs to population seasonal fecundity and λ within each species. We then evaluate whether these direct and indirect predation costs differ among species as a function of average predation rates or within-season residual-reproductive value.

METHODS

We monitored nests and measured reproductive traits for songbird species from 16 May to 15 August, 2009–2014, on 20 forest stands in western Montana, USA (LaManna et al. 2015, LaManna and Martin 2016). Nest-predation rates varied along a natural habitat gradient (LaManna et al. 2015). We searched for nests of all bird species and obtained sufficient data for 10 single- and multiple-brooded species to estimate changes in reproductive rates and success along the natural gradients (Table 1; Appendix S1: Table S1). Methods for monitoring nests, assessing nest fate, and measuring reproductive traits can be found in LaManna et al. (2015) and LaManna and Martin (2016). We calculated perceived-predation risk (hereafter predation risk) for each nest by estimating daily nest-predation rates specific to each forest stand, year, and time of year (i.e., day of the year), and assigned each nest a risk value based on its forest stand, year, and time of year (Shaffer 2004, LaManna and Martin 2016). Forest stand, year, and time of year explained significant variation in daily nest predation rates (DNPR) for all but one of the ten species (white-crowned sparrow; Appendix S1: Table S1). Moreover, increases in nest predation risk were found to be associated with shorter nesting periods and reduced numbers of fledglings from non-predated nests, but these responses varied among species (Appendix S1: Fig. S1; LaManna and Martin 2016). While this measure of nest predation risk is based on actual nest predation rates, we also experimentally increased perceived predation risk with playbacks of predator vocalizations for four of the species included here, and these playbacks largely confirmed the responses to risk observed along the natural risk gradients (LaManna and Martin 2016).

These direct (i.e., DNPR) and indirect (i.e., proximate changes in nesting period length (NPL) and numbers of fledglings from non-predated nests) predation effects have different but interacting influences on seasonal fecundity. Daily nest predation rates determine the daily survival probability of a nest, and such direct predation costs are generally the only variables used to describe differences in predation effects across species (e.g., Martin 1995, Relyea 2001). Nesting period length determines the number of days a nest is exposed or susceptible to

TABLE 1. Life-history parameters of 10 songbird species used in demographic models.

| Common name | Scientific name | Mean DNPR | Mean FLDG | Annual adult survival [†] | Nesting season (d) | Nesting period (d) | Time after nest failure [‡] | Time after nest success [‡] | Multiple/Single-brooded |
|------------------------|-------------------------------|-----------|-----------|------------------------------------|--------------------|--------------------|--------------------------------------|--------------------------------------|-------------------------|
| Warbling Vireo | <i>Vireo gilvus</i> | 0.0085 | 2.85 | 0.557 | 25 | 28 | 8 | — | Single |
| MacGillivray's Warbler | <i>Oporornis tolmiei</i> | 0.0091 | 2.98 | 0.491 | 13 | 23 | 7 | — | Single |
| Dusky Flycatcher | <i>Empidonax oberholseri</i> | 0.0166 | 3.29 | 0.577 | 30 | 32 | 7 | — | Single |
| Lazuli Bunting | <i>Passerina amoena</i> | 0.0213 | 3.07 | 0.517 | 12 | 22 | 7 | — | Single |
| Dark-eyed Junco | <i>Junco hyemalis</i> | 0.0287 | 3.38 | 0.565 | 43 | 26 | 4 | 7 | Multiple |
| Swainson's Thrush | <i>Catharus ustulatus</i> | 0.0302 | 2.68 | 0.595 | 25 | 28 | 7 | — | Single |
| Chipping Sparrow | <i>Spizella passerina</i> | 0.0312 | 3.30 | 0.566 | 43 | 23 | 5 | 9 | Multiple |
| White-crowned Sparrow | <i>Zonotrichia leucophrys</i> | 0.0329 | 2.75 | 0.504 | 25 | 24 | 5 | 7 | Multiple |
| American Robin | <i>Turdus migratorius</i> | 0.0385 | 3.31 | 0.546 | 54 | 28 | 6 | 7 | Multiple |
| Lincoln's Sparrow | <i>Melospiza lincolni</i> | 0.0388 | 3.05 | 0.554 | 23 | 24 | 6 | — | Single |

Notes: Mean daily nest predation rate (DNPR), number of fledglings per non-depredated nest at mean DNPR (Mean FLDG), annual adult survival, length of nesting season (number of days in which the middle 90% of nests were observed to initiate nests), nesting period (number of days between first egg laid and nest fledging), time (in days) required to wait after nest failure before renesting, time (in days) required to wait after nest success before renesting (for multiple-brooded species), and whether a species is single or multiple brooded are provided for each species.

[†] Survival estimates from Martin (1995) or unpublished capture-recapture estimates (T. E. Martin, unpublished data).

[‡] Times to wait before renesting after nest failure and success are from Lloyd et al. (2005) or assumed 7 d if no data available.

predation. These two variables combine to determine the probability that a given nest will fledge offspring, such that:

$$\text{Probability of a nest fledging young} = (1 - \text{DNPR})^{\text{NPL}}$$

We found that birds nesting in areas with higher predation risk (higher DNPR) also had behavioral responses that shortened NPL (Appendix S1: Fig. S1; LaManna and Martin 2016), potentially mitigating costs from increases in predation rates on the probability of nest success (according to the equation above). Moreover, if a nest was successful and fledged young, we also found that non-predated nests with higher predation risk (higher DNPR) fledged fewer offspring than non-predated nests with lower predation risk (Appendix S1: Fig. S1; LaManna and Martin 2016). Thus, while nests with higher predation risk (higher DNPR) have shorter nesting periods, which might mitigate the probability that they fledge young at all, they also fledged fewer young if they were successful. However, the combined influence of these three variables (DNPR, NPL, and number of fledglings per non-predated nest) on seasonal fecundity remains unclear without demographic models that incorporate all of these direct and indirect predation effects. In addition, nesting pairs whose initial nests fail can nest again within a season as long as time allows, and species that are multiple-brooded can nest again

after a successful nest if time allows. Our demographic models incorporated this life-history difference in the number of broods per year among species, which can heavily influence demography and fitness outcomes among species in nature (Nagy and Holmes 2005). All of these factors combine to determine mean seasonal fecundity of a population, which is a key demographic parameter influencing population growth rates (Pulliam 1988, Lloyd et al. 2005).

We estimated mean seasonal fecundity as the annual production of female fledglings per pair per breeding season (β ; see Pulliam 1988, Lloyd et al. 2005). A simple individual-based model (1×10^5 iterations, each iteration representing an individual breeding pair) was used to estimate β for each species under three scenarios: (1) no predation, (2) direct predation effects only, and (3) direct and indirect predation effects. In the no-predation model, DNPR were set to zero for all individuals of all species, and NPL and the number of fledglings per non-predated nest were set to the values associated with zero nest predation risk (i.e., DNPR = 0) for each species (Appendix S1: Fig. S1; LaManna and Martin 2016). In the model that incorporated only direct predation effects (hereafter direct-only model), we randomly assigned each individual a DNPR from the observed distribution of DNPR for that species, but NPL and the number of fledglings per non-predated nest were always set to the values associated with zero nest predation risk for each

species (Appendix S1: Fig. S1; LaManna and Martin 2016). Finally, in the model that incorporated both direct and indirect predation effects (hereafter direct-and-indirect model), we used the same randomly assigned DNPR values from the direct-only model, but NPL and the number of fledglings per non-predated nest were allowed to vary and were set to the values associated with a nest's predation risk (Appendix S1: Fig. S1; LaManna and Martin 2016).

For all three models (no-predation, direct-only, and direct-and-indirect), each individual had the observed species-specific nesting season duration in which to initiate a nest (Appendix S1: Fig. S2). Species differ in the length of time over which they will initiate nests (Martin 2007). We calculated the observed nesting season duration for each species as the number of days between first and last nests initiated in a season (using all nests in our dataset; Appendix S1: Table S1), but excluding the earliest and latest 5% of nests because these represent outlier individuals, as in Martin (2007). Each model iteration had the following rules: (1) all individuals began laying on day 1 of the nesting season; (2) each day, nests failed with a probability equal to the given DNPR; (3) individuals whose nests failed re-laid after waiting a species-specific number of days based on the literature (Table 1), unless the end of the laying season has been reached; (4) nests that survived the entire nesting period (i.e., NPL) fledged the number of young associated with zero DNPR in the no-predation and direct-only models, and fledged the number young associated with their given DNPR in the direct-and-indirect model (Appendix S1: Fig. S1); (5) following a successful nest, multiple-brooded species were allowed to attempt another brood after waiting a species-specific number of days based on the literature (Table 1); (6) single-brooded species were not allowed to initiate a second brood following a successful one (Table 1; Appendix S1: Fig. S2). After running 1×10^5 iterations for each species under each of the three model scenarios (no-predation, direct-only, and direct-and-indirect), we split those 1×10^5 iterations into 100 replicate populations of 5,000 breeding pairs. This population size (5,000) approximately reflects the mean breeding-pair density (0.433 pairs/ha) across our 10 study species in an area approximately the size of one of the watersheds in which we monitored nests (Tenderfoot Creek watershed: $\sim 120 \text{ km}^2$ or 12,000 ha). We then calculated seasonal fecundity for each of these simulated populations as the mean number of female fledglings per female.

Because adult and juvenile survival rates can differ among species and influence the relative importance of seasonal fecundity to population growth rates (λ), we calculated the effect of direct, indirect, and cumulative predation effects in terms of changes to λ and not seasonal fecundity. However, we emphasize that seasonal fecundity was the only parameter subject to variation in our model, and changes in λ reported here therefore do not involve potential direct and indirect predation

influences on adult or juvenile survival. For each value of population seasonal fecundity (β) from the no-predation, direct-only, and direct-and-indirect models above, we calculated λ with the following equation: $\lambda = P_A + P_J\beta$, where P_A is the probability of annual adult female survival, P_J is the probability of juvenile-female survival from fledging to the following breeding season (Pulliam 1988). We used annual adult-survival estimates (P_A) from previous studies (Table 1), and assumed juvenile-female survival (P_J) to be 50% of adult survival, as hypothesized for north-temperate passerines (Greenberg 1980, Temple and Cary 1988, Lloyd et al. 2005). We then measured the change in λ due to direct-predation costs only (λ from the no-predation model minus λ from the direct-only model) and the change in λ due to both direct and indirect predation effects (λ from the no-predation model minus λ from the direct-and-indirect model). We determined the contribution of indirect predation effects to λ by subtracting the change in λ due to direct predation mortality from the change in λ due to cumulative predation effects. In some cases, indirect predation effects had a net-positive influence on λ . For these species, λ from cumulative predation effects was higher than λ from direct costs only. Thus, these species have a positive value for λ due to indirect predation effects, indicating that behavioral responses to increased predation risk ameliorated the negative influences of higher direct predation rates on seasonal fecundity.

We compared the relative influence of direct and indirect predation costs on seasonal fecundity by calculating the weighted mean effects across species. We also calculated the weighted mean effects separately for single- and multiple-brooded species. These mean effects were weighted by the error around estimates of predation costs for each species (LaManna and Martin 2016). We used linear models that accounted for phylogenetic history (package "caper"; Orme et al. 2013) to test if average direct-predation rates predicted direct, indirect, or cumulative predation costs to seasonal fecundity across species. We used identical linear models that accounted for phylogenetic history to test if direct, indirect, or cumulative predation costs to seasonal fecundity differed among species with single- or multiple-brooded behavior. For these models, we used a majority-rule consensus tree computed with program Mesquite (Maddison and Maddison 2015) from 1,000 trees obtained from Bird-Tree.org (Jetz et al. 2012).

RESULTS

Not surprisingly, effects of direct-predation mortality on seasonal fecundity reduced population growth rates (represented by λ) for all species (Fig. 2) and accounted for substantial demographic costs across species (red bars in Fig. 2). Indirect predation effects on seasonal fecundity resulting from behavioral responses to increased perceived risk further reduced λ for six of 10 species (orange bars in Fig. 2). Yet the relative

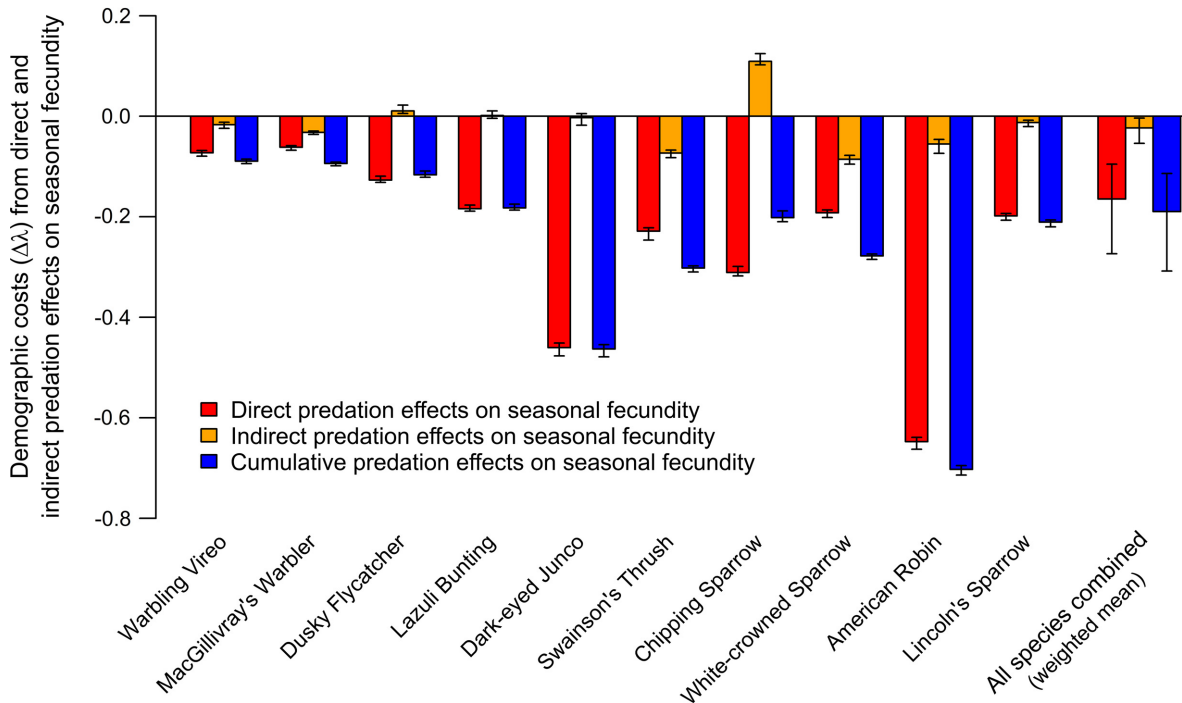


FIG. 2. Demographic costs (λ) from predation effects on seasonal fecundity due to direct predation mortality (red or left bars), indirect predation effects (i.e., costs from behavioral responses to perceived predation risk; orange or middle bars), and cumulative direct and indirect predation effects (blue or right bars). Average demographic costs from indirect, direct, and cumulative effects on seasonal fecundity ($\pm 95\%$ confidence intervals) are weighted by the error around estimates of predation costs for each species. Species in are arranged in order of increasing average direct predation rates.

contributions of direct and indirect predation effects to cumulative predation costs differed widely among species. For four species (MacGillivray's warbler, Swainson's thrush, white-crowned sparrow, and American robin), indirect predation effects on seasonal fecundity contributed to substantial reductions in λ beyond direct predation costs (Fig. 2). For two other species (warbling vireo and Lincoln's sparrow), indirect predation effects on seasonal fecundity were significant, but relatively minor compared to direct predation costs (Fig. 2). Yet for two species (lazuli bunting and dark-eyed junco), indirect-predation costs were insignificant, and behavioral responses to increased predation risk actually had a net demographic benefit for two species (dusky flycatcher and chipping sparrow), mitigating direct predation costs (Fig. 2). Thus, demographic costs from direct and indirect predation effects on seasonal fecundity were highly variable across species, but direct effects generally had a greater influence on λ than indirect effects.

Across species, direct-predation mortality was the dominant influence on demographic costs from reductions in seasonal fecundity (Fig. 2). When averaged across species, demographic costs from direct and indirect predation effects accounted for 87.6% and 12.4% of cumulative costs, respectively (Fig. 2). This result was further verified by relationships between average direct-predation rates and demographic costs from cumulative

predation effects on seasonal fecundity across species (Fig. 3). As hypothesized in Fig. 1d, demographic costs from both direct predation effects (Fig. 3a) and cumulative predation effects (Fig. 3c) increased with average direct-predation rates across species. Demographic costs from indirect predation effects on seasonal fecundity were relatively small compared to direct costs (Fig. 2), unrelated to average direct-predation rates across species (Fig. 3b), and had little influence on the relationship between direct predation rates and cumulative-predation costs (Fig. 3a, c).

Life-history differences appeared to influence the relative importance of direct and indirect predation effects on seasonal fecundity across species. Demographic costs from direct (difference \pm SE = -0.257 ± 0.085 ; $P = 0.017$; Fig. 4a) and cumulative (difference \pm SE = -0.246 ± 0.094 ; $P = 0.031$; Fig. 4b) predation effects were greater for multiple-brooded species than for single-brooded species, likely reflecting higher average daily nest-predation rates for multiple- than for single-brooded species. In contrast, indirect predation effects contributed significantly to cumulative demographic costs among single-brooded species but not among multiple-brooded species (Fig. 4c). However, single- and multiple-brooded species did not differ in the relative contribution of indirect effects (difference \pm SE = -0.159 ± 0.165 ; $P = 0.363$; Fig. 4c), likely reflecting high variability in indirect costs

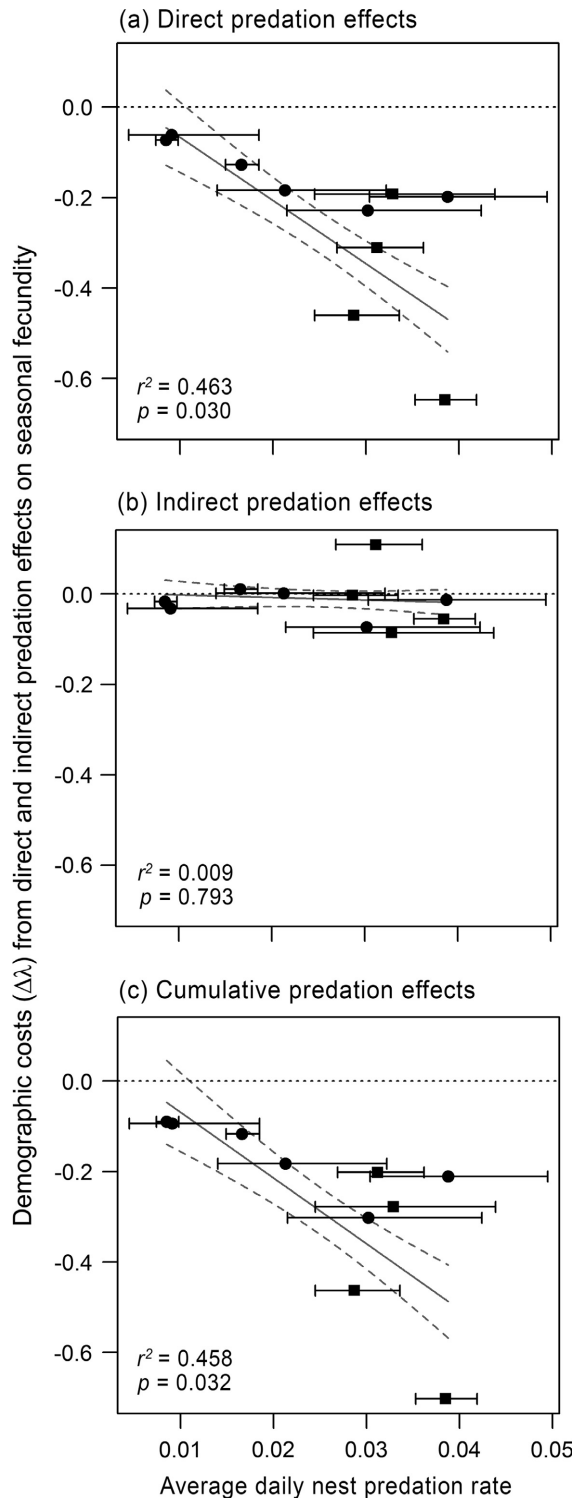


FIG. 3. Relationships across 10 breeding songbird species between average direct-predation rates (\pm SE) and demographic costs from (a) direct, (b) indirect, and (c) cumulative predation effects on seasonal fecundity. Solid gray lines indicate best-fit regression lines (dashed gray lines are \pm SE) informed by phylogenetic relationships among songbird species.

for multiple-brooded species and/or small sample sizes. Ultimately, demographic costs from cumulative and direct predation effects on seasonal fecundity appear to be relatively more important for multiple-brooded species, and indirect predation effects appear to be relatively more important for single-brooded species.

DISCUSSION

Indirect demographic costs from predation risk have received increased attention in recent years (Relyea and Auld 2004, Preisser et al. 2005, Fontaine and Martin 2006a, Creel and Christianson 2008, Zanette et al. 2011, LaManna and Martin 2016), but the reason why these costs vary among species has not been examined. We found that reductions in seasonal fecundity from behavioral responses to increased perceived predation risk had variable effects on fitness across 10 songbird species (Fig. 2). At one extreme, indirect predation costs represented nearly one-third of cumulative predation costs for two of 10 species (Fig. 2). Yet four species experienced no reductions in estimated population growth rates (λ) from indirect predation effects, and behavioral responses to increased perceived predation risk actually had a net λ benefit (i.e., mitigated direct costs) for two of these species (Fig. 2). Although sample sizes were small for some of the species presented here (Appendix S1: Table S1), variability in predation risk and the effects of risk on traits were significant for nearly all species studied (Appendix S1: Table S1; LaManna and Martin 2016). Importantly, our results and inferences are qualitatively similar regardless of whether species with small sample sizes are removed from our analyses. Thus, the influence of indirect-predation effects on seasonal fecundity varied widely among species, but were generally less important than direct predation mortality.

Demographic costs from indirect predation effects on seasonal fecundity were roughly one-eighth the magnitude of direct costs when averaged across all 10 songbird species (Fig. 2). In contrast, a meta-analysis across mostly aquatic invertebrate species found that indirect-predation effects were as strong, if not stronger, than direct-predation effects on prey fecundity, survival, density, and population growth rates (Preisser et al. 2005). Yet, the same meta-analysis also observed generally weaker indirect costs in the few terrestrial species examined (all grasshoppers). Stronger indirect than direct costs from predation in aquatic compared to terrestrial systems might be due to more readily available chemical cues from predators in water (Preisser et al. 2005). Stronger indirect-predation costs in aquatic systems might also be due to the suspected higher prevalence of trophic cascades in water (Strong 1992) because trophic cascades have been generally associated with stronger indirect costs (Preisser et al. 2005). Other confounding factors among studies (e.g., differences in life-stages of predators and prey, predator and prey life-histories, predator-hunting

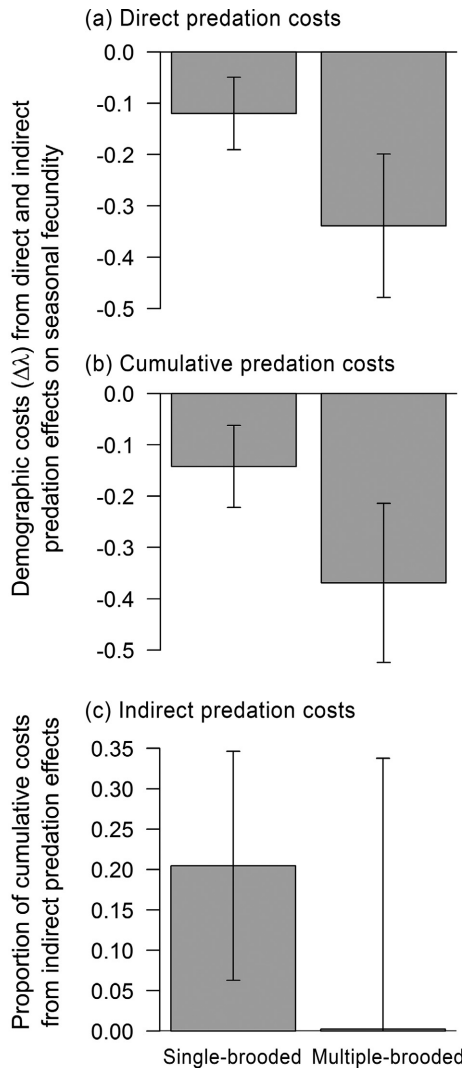


FIG. 4. Comparisons of demographic costs (λ) from predation effects on seasonal fecundity among species with single- and multiple-brooded behavior. Average demographic costs from (a) direct and (b) cumulative predation effects on seasonal fecundity ($\pm 95\%$ confidence intervals) were greater for multiple-brooded species. (c) However, indirect predation effects contributed to a significant proportion of cumulative predation costs for single-brooded but not multiple-brooded species ($\pm 95\%$ confidence intervals). A value near zero for the proportion of cumulative predation costs from indirect predation effects for multiple-brooded species indicates that, on average, indirect-predation effects neither added to nor mitigated costs from direct predation mortality. Average demographic costs from indirect, direct, and cumulative effects on seasonal fecundity ($\pm 95\%$ confidence intervals) are weighted by the error around estimates of predation costs for each species.

strategies, and environmental conditions) could explain stronger indirect predation costs in aquatic systems. Moreover, experimental studies that manipulate predator cues without quantifying their naturally occurring magnitude or duration potentially expose prey to cues exceeding those encountered in natural systems (Peacor 2006,

Chivers et al. 2013, Janssens and Stoks 2014, Van Buskirk et al. 2014). If so, these studies may overestimate indirect costs (Fraker 2009). The simulation models used here, however, are based on measurements from natural gradients in nest predation risk and should be robust to this concern. Thus, our results support the hypothesis that direct-predation mortality has a stronger relative influence on aspects of demography (e.g., seasonal fecundity) than indirect-predation effects in terrestrial systems.

While we examined predation effects on seasonal fecundity, predation can have both direct and indirect influences on other demographic and fitness components (Preisser et al. 2005, Cresswell 2008, 2011). For example, due to the scope of our study, we were unable to evaluate the influence of predation risk on other aspects of reproduction and parental care of offspring, including breeding-territory selection, altered foraging by adults, or changes in offspring quality from reduced food delivery (e.g., Fontaine and Martin 2006b, Cresswell 2011, Emmering and Schmidt 2011, Hua et al. 2014). Potential direct predation costs elsewhere in the life cycle were also not evaluated here, including direct predation of fledglings, juveniles, and adults (Pulliam 1988, 2000, Martin 2015). Thus, indirect predation effects might contribute more to demographic costs relative to direct mortality in other stages of the life cycle not examined here. Nonetheless, we found that direct predation contributed more to cumulative seasonal fecundity costs than indirect effects.

Demographic costs from cumulative and direct predation effects on seasonal fecundity were much higher for multiple- than for single-brooded species (Fig. 4a, b). This result suggests that species with higher probability of repeat breeding within a season, or greater within-season residual-reproductive value (Williams 1966, Clutton-Brock 1984, Clark 1994), are more strongly influenced by direct than by indirect predation costs during reproduction. Longer breeding seasons, and associated additional breeding opportunities within a season, likely also increased the relative importance of direct predation mortality for multiple-brooded species (Martin 2007). In addition, reductions in nesting-period lengths in riskier habitat decreased probability of time-dependent nest mortality more for multiple-brooded species than for single-brooded species (LaManna and Martin 2016). These greater fitness benefits from behavioral responses to perceived risk likely reduced the magnitude of indirect predation costs for multiple-brooded species relative to single-brooded species (Fig. 4c). Thus, our results suggest that the relative importance of direct predation effects increases and the relative importance of indirect predation effects decreases as within-season residual-reproductive value increases across species.

While the relative demographic costs from direct and indirect predation effects on seasonal fecundity varied across species as a function of their life-history strategies, cumulative predation costs increased with average direct predation rates across species (Fig. 3c). In contrast,

indirect predation costs did not increase with direct predation rates across species, and were relatively weaker than direct costs (Fig. 3a, b). Thus, indirect costs may not need to be measured in studies examining predation effects on demography or trait evolution across many terrestrial species (e.g., Reznick and Endler 1982, Martin 1995, Ghalambor and Martin 2001, Relyea 2001, Ghalambor et al. 2013) because our results suggest that average predation rates can index overall predation selection during reproduction (Martin and Briskie 2009).

Nevertheless, indirect fitness costs from behavioral responses to perceived predation risk are important to consider. Demographic costs from indirect predation effects on seasonal fecundity were a third of cumulative predation costs for two of ten species studied here and even mitigated direct predation mortality for two other species (Fig. 2). Thus, studies examining predation costs on one or a few species should attempt to measure indirect predation costs/benefits as well as direct predation mortality. Habitat suitability, population-growth rates, and predation selection on trait evolution are often measured for species without taking indirect predation costs into consideration (Creel and Christianson 2008), and any potential benefits of behavioral responses to risk are often overlooked. Ignoring indirect costs may have particularly worrisome implications for the designation and conservation of suitable habitat for threatened or endangered species, especially if these species have strong indirect relative to direct predation costs (e.g., MacGillivray's warbler in this study). Overall, our results demonstrate that reductions in seasonal fecundity resulting from behavioral responses to perceived predation risk can alone cause demographic costs across species, but the relative influence of direct and indirect predation costs on demography varies among species as a function of their life-history strategies. However, our results also indicate that direct predation mortality has a dominant influence on seasonal fecundity across terrestrial vertebrate species.

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