

LETTER

Costs of fear: behavioural and life-history responses to risk and their demographic consequences vary across species

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Abstract

Behavioural responses to reduce predation risk might cause demographic ‘costs of fear’. Costs differ among species, but a conceptual framework to understand this variation is lacking. We use a life-history framework to tie together diverse traits and life stages to better understand interspecific variation in responses and costs. We used natural and experimental variation in predation risk to test phenotypic responses and associated demographic costs for 10 songbird species. Responses such as increased parental attentiveness yielded reduced development time and created benefits such as reduced predation probability. Yet, responses to increased risk also created demographic costs by reducing offspring production in the absence of direct predation. This cost of fear varied widely across species, but predictably with the probability of repeat breeding. Use of a life-history framework can aid our understanding of potential demographic costs from predation, both from responses to perceived risk and from direct predation mortality.

Keywords

Anti-predator, behaviour, birds, demographic cost, dependent offspring, development, growth, life history, predation, reproductive success.

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INTRODUCTION

Organisms across taxa adjust behaviours and life-history traits in response to increased perceived predation risk (e.g. Werner *et al.* 1983; Lima & Dill 1990; Kotler *et al.* 1991; Fontaine & Martin 2006). Behavioural and life-history responses to risk are expected to decrease the probability of mortality from direct predation (Creel & Christianson 2008; Martin & Briskie 2009). This crucial benefit can be offset by demographic costs resulting from responses to risk (Karels *et al.* 2000; Nelson *et al.* 2004; Preisser *et al.* 2005; Hodges *et al.* 2006). Yet evidence for these ‘costs of fear’ (*sensu* Martin 2011) comes predominantly from artificial invertebrate and aquatic systems (Preisser *et al.* 2005). Moreover, single-species tests indicate that costs can vary substantially across species (Barry 1994; Morrison 1999; Downes 2001; Eklöv & VanKooten 2001; Zanette *et al.* 2011; Hua *et al.* 2014), although the extent to which differences in methodological approach among investigators contribute to this variation is unknown. Comparative studies of species exposed to standardised increases in environmental risk are needed to better understand the extent of variation in costs among species.

An evolutionary framework may help to understand why species differ in their proximate responses to risk and associated costs (Clark 1994; Relyea 2001; Martin & Briskie 2009; Boonstra 2013). Specifically, evolved life-history differences (e.g. reproductive strategies) among species may attenuate or exaggerate behavioural responses to increased perceived risk or cause species to respond to risk in variable ways, leading to differing costs among species. For example, species have evolved under different levels of predation pressure (Martin 1995; Fontaine *et al.* 2007). Demographic costs of fear might increase with average predation rates across species because

the magnitude of behavioural responses to risk can increase for species that evolved under higher average predation rates (Sih 1987; Lima & Dill 1990; Relyea 2001; Martin & Briskie 2009; Ghalambor *et al.* 2013). Other aspects of life histories may also influence the relative costs from proximate responses to risk among species. For example, length of development time can influence predation rates because it is a time-dependent source of mortality (Martin 1995; Warkentin 1995; Arendt 1997; Chivers *et al.* 2001), such that behavioural responses to alter development time may affect demographic costs. However, species that have already evolved shorter development times may be physiologically constrained from proximately reducing development times any further in response to environmental increases in risk (Martin & Briskie 2009). Offspring size or number may also be adjusted in riskier environments with subsequent consequences for offspring production (e.g. Zanette *et al.* 2011). Yet, the relative costs of reduced numbers of offspring in a current attempt may be offset by repeat breeding (Williams 1966; Clutton-Brock 1984; Slagsvold 1984; Clark 1994; Martin & Briskie 2009; Boonstra 2013). Adults of species that have evolved a higher probability of repeat breeding have greater residual reproductive value and may respond to increased environmental risk in a way that reduces reproductive effort in the current attempt and enhances the odds of surviving to the next breeding attempt (asset protection principle; Clark 1994). Thus, an evolutionary framework may help explain variation in proximate responses to increased risk and associated costs among species, but is largely unexamined.

Breeding songbirds provide an excellent system for examining differences in phenotypic and demographic responses to predation risk across species. Songbird species differ in food delivery rates to offspring, growth strategies, incubation

behaviours, clutch size and egg size (reviewed in Martin & Briskie 2009). Shifts in these traits in response to environmental increases in risk may vary among species depending on the average predation rate under which they evolved (Cheng & Martin 2012; Ghalambor *et al.* 2013), and songbird species differ strongly in average nest predation rates (Martin 1995). For example, parent birds feed offspring less often with increased risk to reduce the likelihood that a visually oriented predator will detect their nest or because they forgo foraging for vigilance (Skutch 1949; Lima & Bednekoff 1999; Martin *et al.* 2000; Ghalambor & Martin 2001). Yet, species that evolved under higher average predation rates reduced feeding more than species that evolved under lower average predation rates (Ghalambor *et al.* 2013). Moreover, fewer feeding trips led to offspring starvation in one species (Zanette *et al.* 2011) but not in another (Hua *et al.* 2014). Extent of such responses and consequences may vary with other life-history traits such as residual reproductive value as reflected by the propensity for repeat breeding within a year (Slagsvold 1984; Clark 1994), and songbird species differ strongly in this trait (Nice 1957; Martin 1995). Species that nest more times per year might reduce reproductive effort more for a current clutch (i.e. fewer or smaller eggs) in risky habitat to save resources for later nesting attempts (Slagsvold 1984; Zanette *et al.* 2006). Because these evolved differences can potentially alter the magnitude and direction of proximate responses to risk and the extent of costs, comparisons among species of the demographic consequences from responses to increased perceived risk need to be examined in the context of this life-history approach.

We used observational and experimental approaches to investigate the extent of variation across songbird species in their responses to increased risk and associated demographic costs. We first examined behavioural and demographic responses from nests that were not consumed by predators along natural nest predation risk gradients for 10 songbird species. We also experimentally elevated perceived risk with predator playbacks for four bird species to directly test predation risk as the cause of trait responses and associated demographic costs. We examined the variation in extent of responses and demographic costs with respect to average predation rates (a proxy for the level of predation under which a species evolved) and life-history strategies. We use our study to provide an initial synthetic framework to integrate diverse traits and life stages to better understand the variation in responses to perceived predation risk and associated demographic costs across species that differ in evolved life histories.

MATERIALS AND METHODS

Natural nest predation gradients

This study was conducted from 16 May to 15 August, 2009–2014, within 20 forest stands that varied in relative composition of deciduous to coniferous vegetation in western Montana, USA (LaManna *et al.* 2015). Nest predation rates varied along this vegetation gradient for all 10 bird species, but some species had greater nest predation in conifer vegetation while others had greater nest predation in deciduous vegetation (Fig. S1; LaManna *et al.* 2015). Thus, nest predation

risk varied across species in opposing directions along the environmental gradient, providing a strong natural back-drop for testing behavioural and demographic responses to predation risk across species.

We searched for nests of all bird species. We obtained sufficient data from 10 species to estimate variation in reproductive traits along the natural risk gradients (Table S1; Fig. S2; LaManna *et al.* 2015). These species have evolved different probabilities of future breeding which affect their residual reproductive value (Clark 1994). Species that only raise one successful brood per year (hereafter, single-brooded species) have a lower probability of future breeding than species that raise more than one successful brood per year (hereafter, multiple-brooded species) because the probability of surviving to the next breeding season is quite low (~40–50%) compared to survival rates during the breeding season (~99%; Sillett & Holmes 2002). If nests of single-brooded species are depredated, they will only attempt to re-nest one or two times per year while multiple-brooded species will generally re-nest as many times as possible within a breeding season (Joseph A. LaManna, Thomas E. Martin, pers. obs.). Thus, the probability that a single-brooded species will re-nest again is much lower than for a multiple-brooded species, yielding higher residual reproductive value for the latter.

We visited nests every 2 days to measure predation rates, but visited nests twice daily around transition dates (e.g. hatch date) to accurately measure incubation and nestling period lengths. Red squirrel (*Tamiasciurus hudsonicus*), chipmunk (*Tamias* spp.), gray jay (*Perisoreus canadensis*), Steller's jay (*Cyanocitta stelleri*) and common raven (*Corvus corax*) were potential nest predators in this system. We measured the following traits at nests: clutch size (number of eggs/nest), egg mass (g), clutch mass (clutch size × egg mass), nest attentiveness (proportion of time parents incubate eggs), incubation period length (days from last egg laid to last egg hatched), hatch success (eggs hatched/eggs laid), number of hatchlings (number of eggs that hatched), total provisioning rates (total parent feeding visits per hour), nestling survival (fledglings/hatchling), nestling period length (days from last egg hatched to last nestling fledged) and number of fledglings. We calculated changes in the probability of nest predation due to any observed changes in incubation and nestling period lengths. We also calculated nestling growth trajectories. We measured nestling mass (g), nestling wing chord length (mm) and nestling tarsus length (mm) for the first 3 days after hatch and every other day thereafter. For detailed methods, see supplemental methods.

Experimental increase in perceived risk

We experimentally increased perceived nest predation risk over the entire nesting period for four of the 10 species during 2012–2014 (Table S1) and compared responses to control nests paired by date and location. These four species were selected because we were able to most successfully implement and replicate the experiment for these species. We identified experimental nests during the early nest-building stage, and placed three speakers (Eco Extreme by Grace Digital, San Diego, CA, USA) with MP3 players (Sansa Clip by

SanDisk, Milpitas, CA, USA) around each nest for 6 h beginning within 30 min of sunrise. We used speakers two of every 3 days, placed speakers in new locations each day (within 8–10 m of the nest), and randomised when speakers played vocalisations in order to reduce habituation to playbacks. To approximate a natural increase in risk, playbacks were only conducted in forest stands with lower average predation rates (Fig. S1) and playback vocalisation rate was tailored to match predator vocalisation rates in our riskier forest stands (Fig. S3). Each speaker played the same ratio of one min vocalisations to 11 min silence, but this was a total of 3 min of vocalisations across all three speakers for every 12 min. We used identical methods for playbacks at spatially and temporally paired control nests, except playbacks at controls were from non-threatening species (Table S2). We used 158 1-minute-long recordings of calls and sounds from nest predators and non-threatening species (Table S2). Playback experiments started in early nest building and continued until the nest was depredated or fledged young. We collected identical data from treatment and control nests as was collected from nests along risk gradients. We also documented if/when nests were abandoned. Only nests found within 2 weeks of average nest initiation for a given species were used in this experiment. For detailed methods, see supplemental methods.

Statistical analyses

We began by assessing responses of each species to environmental increases in perceived predation risk. Along natural risk gradients, we calculated species-specific nest predation rates for each forest stand, Julian date and year using logistic exposure. We then assigned each nest a risk level equivalent to the average predation rate of nests in the same forest stand, year and time of year. These were measures of perceived predation risk for each nest. We used linear mixed models to test for relationships between this measure of risk and all measured reproductive traits for each species with year, forest stand and nest as random factors. We compared different models that included risk, Julian date, clutch size, and egg and nestling age as fixed effects to a null model that contained no fixed effects (see Table S3). Age was included for models describing egg mass, nestling growth and parental provisioning rates because these are known to change predictably with age. For nestling mass, tarsus size and wing chord length, we examined changes in growth rates (K), the timing of growth (inflection time, or t_i) and asymptotic size (A) with increased risk using nonlinear mixed models that estimated changes in growth as a direct function of variation in risk. We compared models using Akaike's information criterion (AIC_c) and evaluated if 95% confidence intervals (CI) of covariates in top-ranked models included zero and assessed cumulative model weight support for each model covariate. Analyses along risk gradients were only conducted for traits sampled from at least five nests of a given species. We also measured effects of any observed changes in incubation or nestling periods on direct predation probability.

We conducted a meta-analysis to determine if proximate responses to risk and demographic costs were consistently

repeated across species. Statistical power might not be strong enough to detect a common risk response or cost within one species. Thus, we increased our power to detect generalised risk responses and costs by calculating average standardised risk responses and costs across all 10 species. Intercept-only ANOVA models calculated these average responses and costs across species, and were weighted according to the error around the standardised effect size of each species' response to risk (standardised regression coefficients *sensu* Schielzeth 2010). We evaluated if these average effect sizes were significantly different from zero, indicating a generalised risk response or demographic cost across species.

We expected changes in nest attentiveness with risk to be negatively correlated with changes in incubation period length across species (Martin *et al.* 2007). We also expected changes in nest attentiveness with risk to be negatively correlated with changes in egg mass across species because parents may need to provide extra provisions to eggs developing at colder temperatures (Martin 2008). We therefore evaluated correlations among their standardised effect sizes across species with weighted ANOVA models identical to those described for meta-analyses above. We also evaluated the relative sensitivity of mass, wing and tarsus growth to changes in per-nestling feeding rate by comparing correlations between changes in per-nestling feeding and the corresponding change in mass, wing and tarsi growth rates. We evaluated all of these across-species correlations with weighted ANOVA models as described above.

We then tested if the magnitude or direction of behavioural and demographic responses to increased risk varied among species as a function of their evolved life histories. We used linear models that accounted for phylogenetic history to test for an association between the magnitude of a given behavioural or demographic response (standardised effect size *sensu* Schielzeth 2010) and the average nest predation rate of a species. We also tested if behavioural responses to risk and associated costs varied across species with different probabilities of future breeding (i.e. multiple- or single-brooded) using an identical phylogenetically informed model.

For the predator-playback experiment, we tested for differences between treatment and control nests for each reproductive trait using ANOVA with a random factor of year. Significance tests were only performed when there was a total sample size (treatment and control) of at least six nests. Separate tests were conducted for each species in the experiment. We tested for differences in growth (K , t_i and A) of mass, wings and tarsi between treatment and control nests using nonlinear mixed models. Finally, we evaluated if nestlings prioritised growth of wings or tarsi by measuring the change in the ratio of wing or tarsus growth rates to mass growth rate in response to experimental increases in predation risk (*sensu* Cheng & Martin 2012). We also assessed if behavioural and demographic responses to risk in the experiment differed among species as a function of their life histories in a similar way as observed along natural risk gradients above. For detailed methods, see supplemental methods.

RESULTS

Natural risk gradients

Tests were based on 1014 nests of 10 songbird species along natural risk gradients (Table S1). Parents responded to increased perceived risk during embryonic development by adjusting behaviours that led to changes in developmental rates (Fig. 1). Bird species generally responded to increased risk by increasing incubation attentiveness (Fig. 1a; Table S4; mean effect size \pm SE = 0.37 ± 0.07 , $P = 0.001$) and shortening incubation periods (Fig. 1c; mean effect size \pm SE = -0.70 ± 0.09 , $P < 0.001$). Greater increases in nest attentiveness along risk gradients were associated with greater reductions in incubation period length across species (Fig. 1d; $r^2 = 0.728$, $P = 0.03$). Shortened incubation periods caused reductions in direct predation probability by as much as 6.4% in riskier environments based on daily predation rates. Thus, nearly all bird species responded to increased risk by increasing the proportion of time spent incubating eggs and shortening embryonic development to thereby reduce the time-dependent risk of nest mortality.

Parent birds also adjusted the size and/or number of eggs per clutch with increased risk. Clutch size increased with risk for three species, decreased for one species and did not change for six species, yielding no general response across species

(mean effect size \pm SE = 0.10 ± 0.08 , $P = 0.223$). However, nearly all species altered egg size with risk (effect size \pm SE = 0.68 ± 0.13 , $P = 0.001$; Fig. 1b). Changes in egg mass were not associated with changes in clutch size ($r^2 = 0.037$, $P = 0.59$), but were marginally and negatively associated with changes in nest attentiveness ($r^2 = 0.324$, $P = 0.09$). Changes in egg mass also differed across species as a predictable function of their residual reproductive value (see below).

Parents adjusted feeding rates in response to increased perceived risk, which affected nestling growth rates (Fig. 2). Five species decreased total parental provisioning trips with risk, although the effect was marginal across species (Fig. 2a; mean effect size \pm SE = -0.16 ± 0.09 , $P = 0.098$). These declines in total provisioning rates and declines in number of young (Fig. 3) combined to yield a mild reduction in per-nestling feeding rates across species (Fig. 2b; mean effect size \pm SE = -0.13 ± 0.07 , $P = 0.094$). Changes in body-mass growth rates along risk gradients were strongly and positively associated with changes in per-nestling feeding rates across species (Fig. 2c). Despite changes in nestling body growth rates, nestling period length did not vary with risk for any species. Changes in tarsus growth rates showed a tendency to increase with per-nestling feeding (Fig. 2d). In contrast, changes in wing growth rates showed no relationship with changes in feeding rate (Fig. 2e, S4; Table S5). Three of three

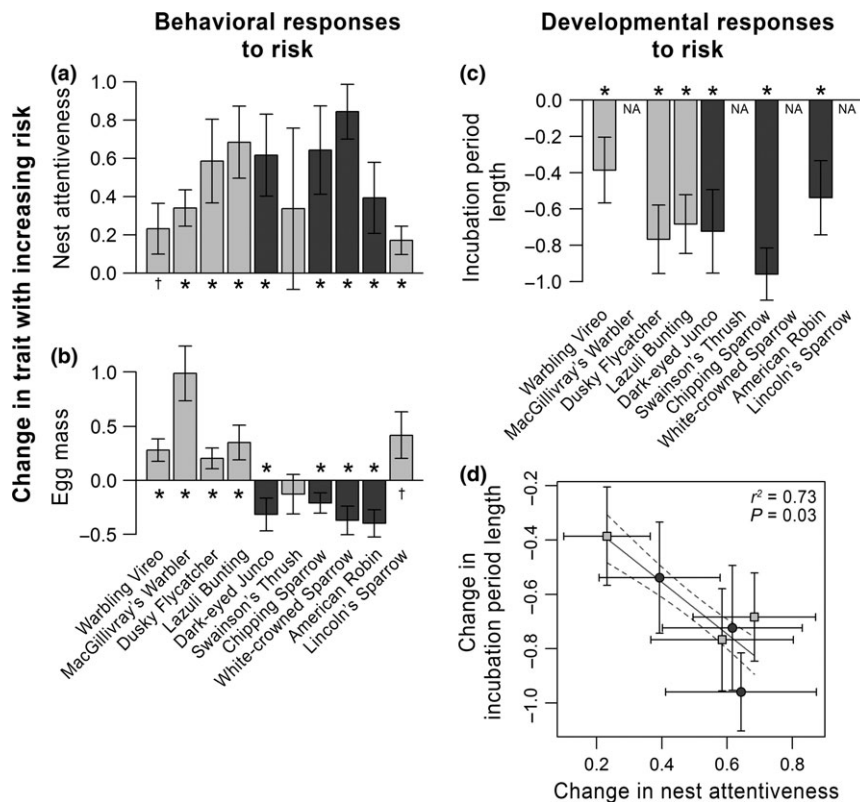


Figure 1 Standardised effect sizes (standardised regression coefficients \pm 1 SE) of behavioural and developmental responses to perceived risk during embryonic development for 10 bird species breeding along natural nest predation risk gradients in western Montana, USA. Parents adjusted (a) nest attentiveness and (b) egg mass in response to increasing risk. Incubation period lengths (c) were shorter in riskier habitats, and stronger increases in nest attentiveness were associated with stronger declines in the length of developmental periods (d). These proximate responses to increased perceived risk differed among single-brooded (light grey) and multiple-brooded (dark grey) species, reflecting evolved differences in residual reproductive value. Species are arranged in order of increasing mean daily nest predation rate. 95% CIs that do not cross zero are denoted as *; 90% CIs that do not cross zero are denoted as †. NA indicates lack of sufficient sample size to analyse an effect (i.e. $n < 5$).

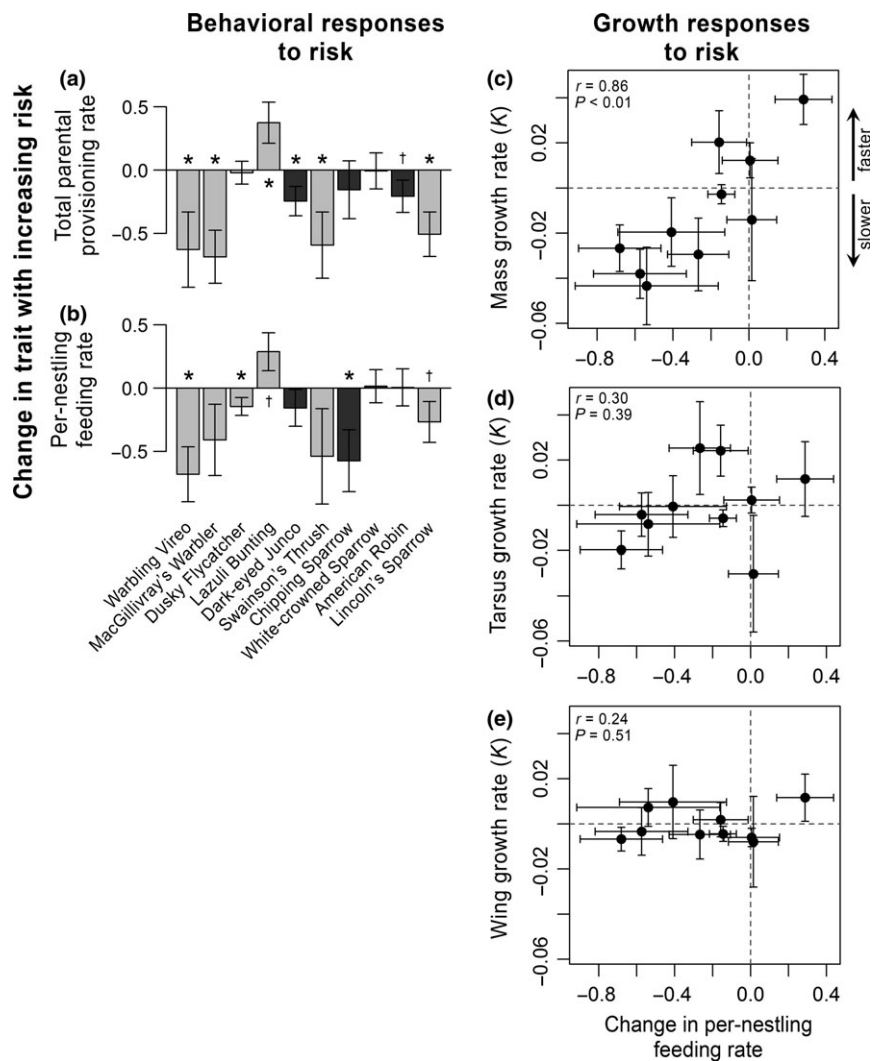


Figure 2 Standardised effect sizes (± 1 SE) for behavioural and growth responses to increased perceived risk during offspring growth for 10 bird species breeding along natural nest predation risk gradients. Parents adjusted (a) total parental provisioning rate and (b) per-nestling feeding rate in response to increased perceived risk. Species are arranged in order of increasing mean daily nest predation rate. 95% CIs that do not cross zero are denoted as *; 90% CIs that do not cross zero are denoted as †. Single-brooded (light grey) and multiple-brooded (dark grey) species are shown. Correlations are also shown between changes in per-nestling feeding rate (Standardised effect sizes ± 1 SE) and changes in nestling (c) mass, (d) tarsus and (e) wing growth rates along natural risk gradients.

species that significantly reduced mass growth rates along risk gradients did not reduce wing growth rates (Table S5). Therefore, species with reduced per-nestling feeding and body-mass growth in riskier habitat nonetheless maintained growth of wings.

The number and survival of offspring changed along natural risk gradients (Fig. 3). While bird species showed no generalised response of clutch size to increased risk (Fig. 3a), the proportion of eggs that hatched (hatch success) generally decreased with risk across species (Fig. 3b; mean effect size \pm SE = -0.22 ± 0.10 , $P = 0.046$). Changes in clutch size and hatch success led to a significant decline in the number of hatchlings along risk gradients within four species (Fig. 3c). Increased risk was also associated with a general decrease in nestling survival in the absence of predation across species (Fig. 3d; mean effect size \pm SE = -0.28 ± 0.10 , $P = 0.020$).

Most critically from a demographic standpoint, reductions in hatch success (Fig. 3b), numbers of hatchlings (Fig. 3c) and nestling survival (Fig. 3d) combined to reduce reproductive success (i.e. number of fledglings from nests that escaped predation) in high-risk habitat across species (Fig. 3e; mean effect size \pm SE = -0.49 ± 0.16 , $P = 0.014$). These demographic costs were especially severe for four species (MacGillivray's warbler, Swainson's thrush, American robin and white-crowned sparrow) and less severe for others (Fig. 3e).

Average daily nest predation rates varied substantially among species (Fig. S5). These differences meant that 20% of warbling vireo nests and 70% of Lincoln's sparrow nests were likely to be depredated given average nesting period lengths. However, neither the magnitude of proximate responses to risk (Table S6a) nor the severity of demographic costs from these responses (Fig. 3f; $r^2 = 0.016$, $P = 0.726$) were related to

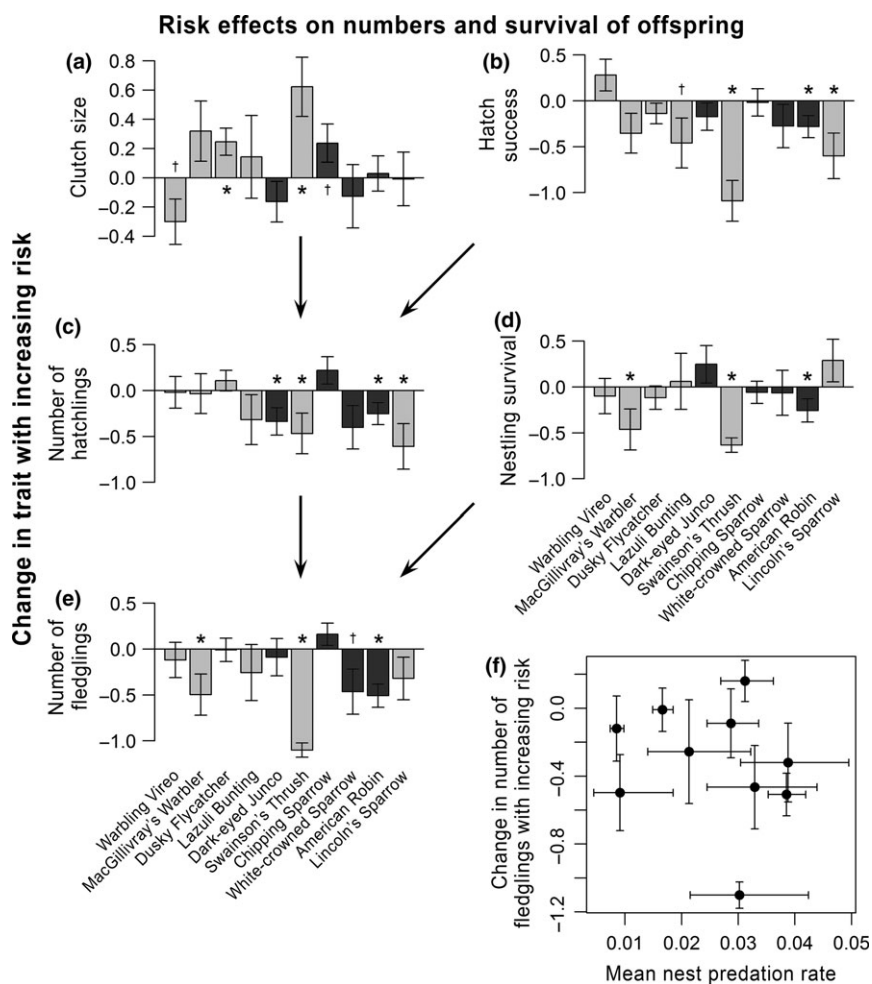


Figure 3 Standardised effect sizes (± 1 SE) for proximate changes in the number of offspring or offspring survival with increasing perceived risk. Changes in (a) clutch size and (b) hatch success (proportion of eggs laid that hatched) combined to influence (c) the change in numbers of hatchlings with increased perceived risk. Changes in (c) the number of hatchlings and (d) nestling survival (fledglings/egg hatched) combined to influence (e) the change in numbers of fledglings with increased perceived risk. 95% CIs that do not cross zero are denoted as *; 90% CIs that do not cross zero are denoted as †. Single-brooded (light grey) and multiple-brooded (dark grey) species are shown. (f) The proximate reduction in numbers of fledglings with increasing perceived risk (± 1 SE) was not associated with the mean nest predation rate (± 1 SE) under which a species evolved (each point is a species).

average predation rates across species. Instead, residual reproductive value appeared to determine the direction and magnitude of behavioural responses during incubation as well as the severity of associated demographic costs across species. Five of six single-brooded species increased egg mass and all four multiple-brooded species decreased egg mass with increased risk (Fig. 1b), which was a significant difference among single- and multiple-brooded species (effect size \pm SE = 0.69 ± 0.13 , $P = 0.001$). Clutch mass also increased for single-brooded species and decreased for multiple-brooded species (effect size \pm SE = 0.81 ± 0.20 , $P = 0.004$). Multiple-brooded species increased nest attentiveness slightly more than single-brooded species in response to increased risk (effect size \pm SE = -0.25 ± 0.13 , $P = 0.089$). This behavioural response to risk led to a slightly larger reduction in probability of direct predation for multiple-brooded species than for single-brooded species (effect size \pm SE = 0.03 ± 0.01 , $P = 0.09$). Observed correlations among trait responses to risk revealed that behavioural responses differed across life stages and

interacted with other behavioural and life-history responses to determine reproductive success (Fig. 4).

Experimental increase in perceived risk

The causal basis of phenotypic changes to risk along the natural risk gradient was largely confirmed by our experimental increase of perceived risk at 95 nests (Figs 5 and 6; Table S7). Experimental increases in risk yielded increased attentiveness and reduced incubation periods by a day or more for all four species tested (Fig. 5a, and b). Multiplying daily mortality probabilities of each species against these decreases in incubation period length indicated that cumulative probabilities of nest mortality were reduced by 3.8–11.3%. Experimentally increased perceived risk did not affect clutch size (Fig. 5c). However, egg mass increased with risk for single-brooded (dusky flycatcher and Swainson's thrush) and decreased for multiple-brooded (chipping sparrow and dark-eyed junco) species (Fig. 5d), as observed along natural risk

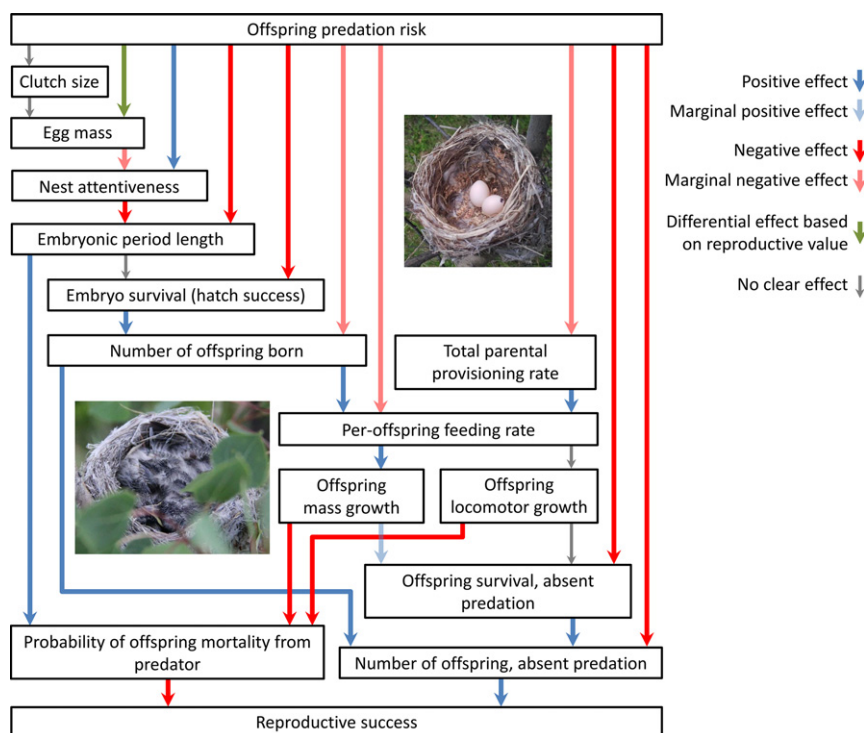


Figure 4 Synthesis of behavioural and life-history responses to increased perceived predation risk along natural risk gradients and associated demographic costs. Offspring predation risk is at the top, and direct and indirect proximate effects of risk on all reproductive traits measured in this study are shown. Correlations between responses of traits to risk and other responses or costs are also shown. Positive effects are in blue, negative in red, and no clear effect is shown with a small grey arrow. Green arrow indicates that the proximate effect of perceived risk on egg mass differs among species as a predictable function of residual reproductive value. This differential effect among species then cascades down through the traits as depicted by arrows.

gradients (Fig. 1b). Nest abandonment rates prior to egg laying and in early incubation were higher under experimentally elevated risk for three species (Fig. 5e), indicating that birds assess and respond to risk even in the earliest nesting stages.

Number of hatchlings did not decline with experimental increases in risk for three of the four species (Fig. 5c), whereas it was a more general effect along natural risk gradients (Fig. 3c). Swainson's thrush, the one species that showed a tendency for reduced number of hatchlings (Fig. 5c), showed a similar response along natural risk gradients (Fig. 3c). Experimentally elevated risk caused the thrush and one other species (chipping sparrow) to decrease total parental provisioning trips (Fig. 6a). The decline in total feeding rate was associated with declines in per-nestling feeding in the sparrow, but the reduction in hatchling numbers for Swainson's thrush yielded an increase in per-nestling feeding (Fig. 6b).

Nestling growth strategies for some species changed with experimental increases in risk across species (Fig. 6) similar to natural risk gradients. Specifically, dusky flycatcher and dark-eyed junco nestlings maintained growth rates of wings and tarsi while mass growth rates declined with elevated risk (Fig. 6c–e). Dark-eyed junco nestlings increased the ratio of wing to mass growth rate ($F = 7.13$, $P = 0.04$) and the ratio of tarsus to mass growth rate ($F = 6.87$, $P = 0.04$) with increased risk. In contrast, chipping sparrows reduced tarsi growth rates, but not mass or wing growth rates, with experimentally elevated risk (Fig. 6c–e). We did not have sufficient data to analyse growth rates for Swainson's thrush nestlings. Thus, species differed in their growth responses to experimentally

increased risk, but generally appeared to maintain growth of wings despite slower growth of mass or tarsi.

Numbers of fledglings from successful nests were unaffected by experimental increases in risk for three species (Fig. 5c), but these species did not show severe demographic costs of fear along natural risk gradients either (Fig. 3). Experimental increases in risk only reduced number of fledglings for Swainson's thrush. While sample size was low for this species, the decline in reproductive success was large (−1.5 fledglings, or 43% decrease in reproductive output) and entirely due to decreased hatch success and not reduced nestling survival (Fig. 5c). Swainson's thrush also had strong demographic costs along the natural risk gradient (Fig. 3). Thus, experimentally induced demographic costs of fear differed among bird species, but these differences were consistent with costs of fear observed along natural risk gradients.

DISCUSSION

Demographic costs generally resulted from behavioural responses to increased perceived predation risk across our 10 study species. Yet, the severity of these costs varied strongly across our study species, verifying that variation in demographic costs observed in other taxa (e.g. contrast Barry 1994; Morrison 1999; Downes 2001; Eklöv & VanKooten 2001; Preisser *et al.* 2005; Zanette *et al.* 2011; Hua *et al.* 2014) are not simply methodological artefacts. This variation highlights the importance of understanding why species differ in both their responses to perceived risk and associated costs.

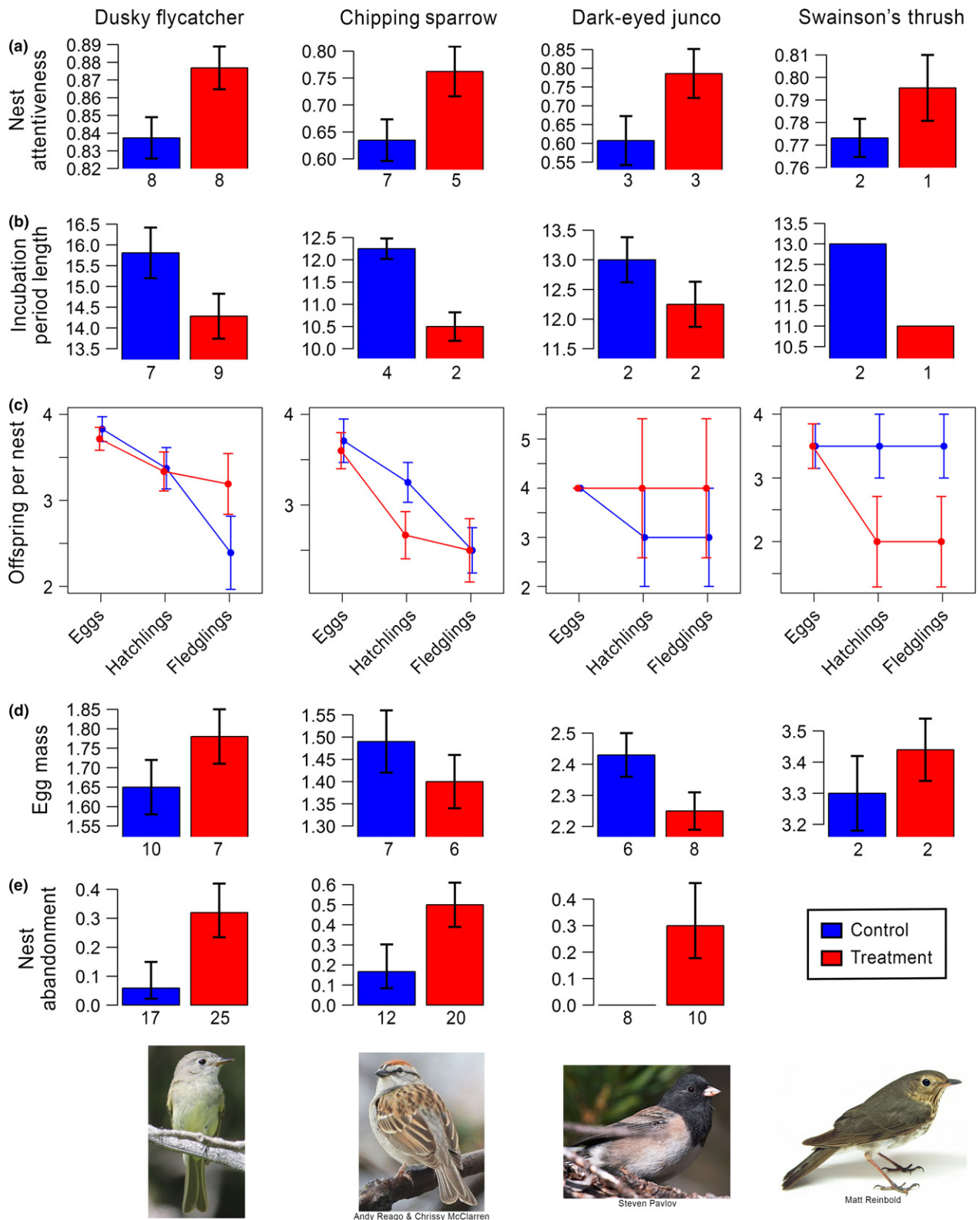


Figure 5 Treatment and control means (± 1 SE) for reproductive traits measured for four bird species in the increased perceived predation risk experiment in western Montana, USA. Traits shown are (a) nest attentiveness, (b) incubation period length, (c) offspring numbers, (d) egg mass and (e) nest abandonment. Sample sizes of treatment and control nests are shown below bars.

Attempts to explain variation in responses and costs from risk among species are rare, but when considered, the focus has been on differences in average predation rates under which

species evolved (Sih 1987; Lima & Dill 1990; Relyea 2001; Martin & Briskie 2009; Ghalambor *et al.* 2013). Yet, the magnitude of responses to risk and associated costs did not

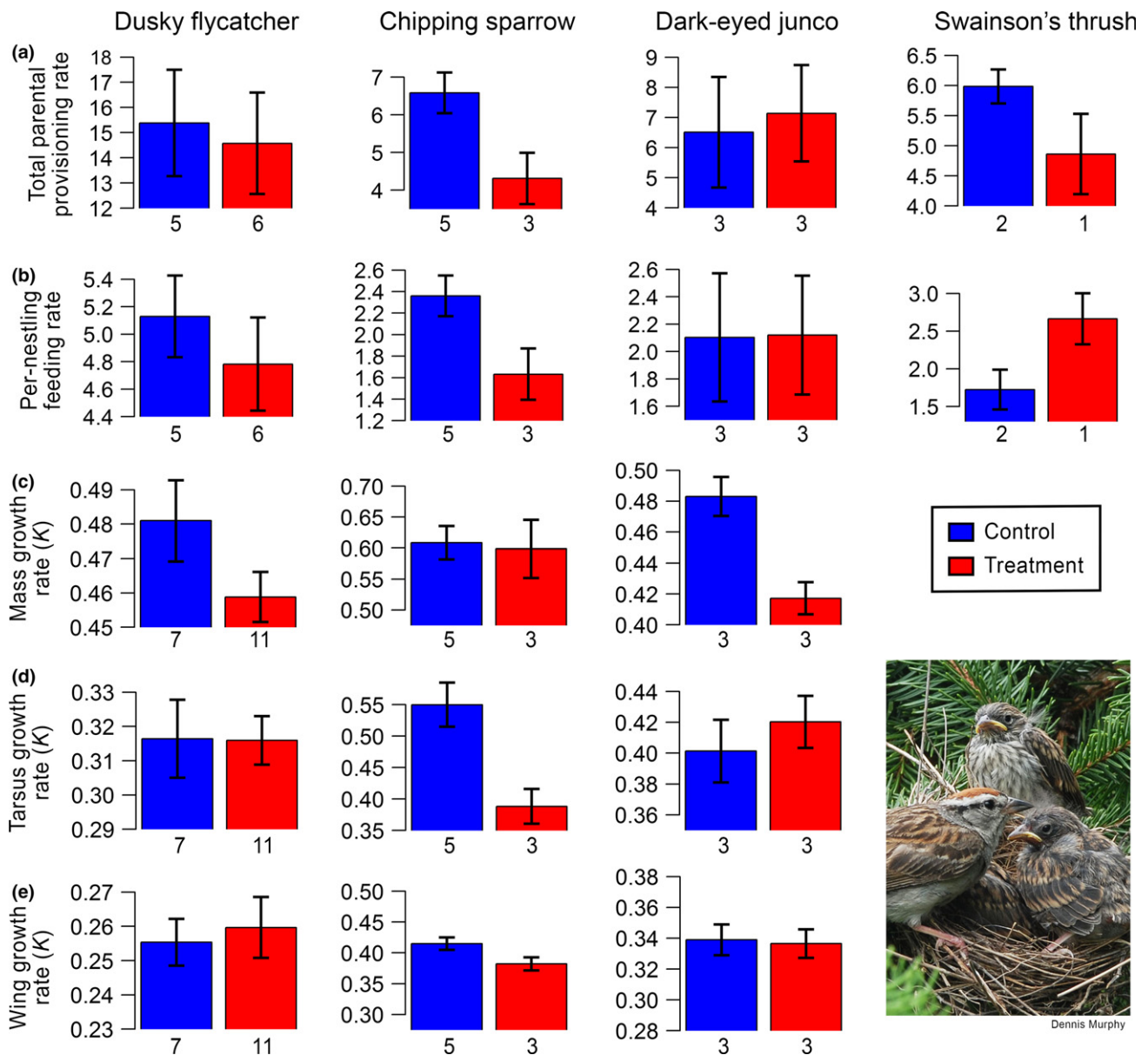


Figure 6 Treatment and control means (± 1 SE) for reproductive traits measured for four bird species in the increased perceived predation risk experiment in western Montana, USA. Responses of (a) total parental provisioning rate, (b) per-nestling feeding rate, and growth rates of (c) mass, (d) tarsi and (e) wings are shown. Sample sizes of treatment and control nests are shown below bars.

increase with average predation rates across species (Fig. 3f). This result suggests that demographic costs of fear may have proportionately less influence on overall reproductive success in species with higher rates of direct predation (Creel & Christianson 2008; Martin & Briskie 2009).

Instead, we show for the first time that responses to perceived risk and associated costs differ among species based on their residual reproductive value (Williams 1966; Clutton-Brock 1984; Clark 1994) as represented by evolved differences in repeat breeding probability. Species with higher probability of repeat breeding reduced investment in propagules and increased parental attentiveness, which yielded shorter development periods and reduced time-dependent predation probability (Table S6b, Fig. 4). Reductions in direct predation probability from behavioural responses to risk are important

because they offset demographic costs from those responses (i.e. fewer offspring). Thus, species with higher residual reproductive value appear to respond to increased perceived predation risk in a way that enhances their ability to reproduce again (also Slagsvold 1984) while minimising costs. These results also suggest that differences in residual reproductive value may be a more important factor determining variation in behavioural and life-history responses to risk and associated costs among species than average predation rates, especially when species differ substantially in the probability of future breeding.

Behavioural responses to perceived risk and associated costs also differed within species across life stages, emphasising the value of considering effects of predation risk in the context of complex life histories (Martin 2015). These behaviours

interacted with one another to determine offspring development and growth rates, offspring survival, predation probability and reproductive success (Fig. 4). Responses such as increased parental attentiveness yielded reduced development time and created benefits in terms of reduced predation probability. Shorter embryonic periods along natural risk gradients and in response to experimentally increased perceived risk reduced predation probability by as much as 6.4 and 11.3% respectively. To our knowledge, this is the first documentation of faster embryonic development in response to increased risk within terrestrial species (Fig. 1c), although faster embryonic development with increased risk has been observed for amphibian eggs (e.g. Warkentin 1995; Chivers *et al.* 2001). Previous studies have largely focused on the demographic costs of fear (Karels *et al.* 2000; Nelson *et al.* 2004; Preisser *et al.* 2005; Hodges *et al.* 2006), but our results suggest that responses to risk do not solely create costs. Instead, costs from risk responses, such as fewer young, trade off with benefits, such as reduced development time and exposure to risk. Such benefits should be necessary for the evolution of costly anti-predator responses.

Other behavioural responses to increased risk, such as reduced parental provisioning, likely also reduce the probability of direct predation (Skutch 1949; Sih 1987; Lima & Dill 1990; Lima & Bednekoff 1999; Martin *et al.* 2000; Brown & Kotler 2004; Eggers *et al.* 2005). However, reduced feeding yielded costs manifested as slower offspring mass growth and reduced survival in the absence of direct predation (Fig. 4), as also observed in fish (Werner *et al.* 1983), snails (Crowl & Covich 1990), amphibians (Skelly & Werner 1990), insects (Ball & Baker 1996) and birds (Massaro *et al.* 2008). Wing growth of nestlings remained relatively constant despite decreases in per-nestling feeding (Fig. 2e) and slower mass growth (Fig. 2c). This result suggests that young of some species sacrifice mass to prioritise growth of wings in situations of increased risk and reduced food. This response is similar to other predator-induced defences that alter morphology to improve the probability of surviving a predator attack (e.g. Barry 1994; Relyea 2001; Cheng & Martin 2012; Martin 2015). In short, declines in reproductive success across our study species support the general contention that perceived predation risk can impose demographic costs (Preisser *et al.* 2005; Zanette *et al.* 2011), but these costs must be weighed against benefits from risk responses.

Other environmental factors, such as reduced food availability, may have contributed to declines in reproductive success along natural risk gradients. Yet, risk varied along the environmental gradient differently for different species, and even in opposite directions, whereas responses observed along risk gradients were consistent with risk as the major cause of this variation across species. Moreover, experimental tests supported the causal role of risk. Demographic costs (Fig. 3e) and nest abandonment (Fig. 5e) from increased perceived risk documented here suggests the existence of strong selection for animals to choose safe breeding and foraging sites when encountering variation in perceived risk. Preferences for safe breeding and foraging sites have been shown in fish, birds and mammals (e.g. Werner *et al.* 1983; Brown & Kotler 2004; Emmering & Schmidt 2011; Basille *et al.* 2015; LaManna

et al. 2015). Therefore, spatial and temporal variation in perceived risk can have far reaching influences on habitat preferences, distributions, behaviours, life-history traits, offspring production in the absence of predation and probabilities of actual predation across taxa.

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AUTHORSHIP

JAL and TEM conceived the study, TEM obtained the funding, and JAL collected the data. JAL executed the statistical analyses and wrote the first draft of the manuscript, and both authors contributed to revisions.

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