# Fear of predators in free-living wildlife reduces population growth over generations

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Correctly assessing the total impact of predators on prey population growth rates (lambda, $\lambda$) is critical to comprehending the importance of predators in species conservation and wildlife management. Experiments over the past decade have demonstrated that the fear (antipredator responses) predators inspire can affect prey fecundity and early offspring survival in free-living wildlife, but recent reviews have highlighted the absence of evidence experimentally linking such effects to significant impacts on prey population growth. We experimentally manipulated fear in free-living wild songbird populations over three annual breeding seasons by intermittently broadcasting playbacks of either predator or nonpredator vocalizations and comprehensively quantified the effects on all the components of population growth, together with evidence of a transgenerational impact on offspring survival as adults. Fear itself significantly reduced the population growth rate (predator playback mean $\lambda = 0.91$, 95% CI = 0.80 to 1.04; nonpredator mean $\lambda = 1.06$, 95% CI = 0.96 to 1.16) by causing cumulative, compounding adverse effects on fecundity and every component of offspring survival, resulting in predator playback parents producing 53% fewer recruits to the adult breeding population. Fear itself was consequently projected to halve the population size in just 5 years, or just 4 years when the evidence of a transgenerational impact was additionally considered ($\lambda = 0.85$). Our results not only demonstrate that fear itself can significantly impact prey population growth rates in free-living wildlife, comparing them with those from hundreds of predator manipulation experiments indicates that fear may constitute a very considerable part of the total impact of predators.

ecology of fear | perceived predation risk | population growth rate | predator–prey interactions | antipredator behavior

Predators kill prey and prey attempt to avoid being killed by predators. Experimentally testing if these impacts on individual prey affect prey population growth rates (lambda, $\lambda$) is critically necessary to correctly assess the total impact predators have on prey populations and hence the importance of predators in species conservation and wildlife management (1–11). That the fear (antipredator behavioral responses) that predators inspire may affect prey population growth has only relatively recently been recognized (1–3, 6, 8–11). Multiple experiments have now established that fear itself can affect fecundity and early offspring survival in free-living wildlife, reducing the number of young produced by over a third, but an impact on population growth has yet to be demonstrated (1, 9–11).

The critical necessity of experimentally testing if fear of predators can affect their prey's population growth rate lies in the fact that even killing by predators cannot simply be assumed to affect prey population growth in free-living wildlife—and indeed it was long generally presumed not to (1, 8, 10, 11). From the 1940s to at least as late as 2010 predators were commonly viewed as little more than scavengers, killing the very young, old, sick, or injured, the so-called "doomed surplus" whose fate did not affect the prey's population growth rate (1, 8, 12). Because fear has to date only been demonstrated to affect the number of very young these too could represent a

"doomed surplus" (1, 11, 12). Alternatively, the total impact of fear on population growth could be far greater than currently indicated, extending even to transgenerational impacts reducing population growth over generations (1, 13–15). This is because the reductions in fecundity and early offspring survival demonstrated to date have primarily been attributable to fear impairing parental investment and care (1, 9, 16–22), and such early developmental stress can be expected to have negative effects later in life (15). Research on song sparrows (*Melospiza melodia*), for example, has shown that experimental food restriction during early development, mirroring fear-induced reductions in parental provisioning, impairs brain development (9, 23), as manifested by offspring singing fewer songs as adults (24), which is predictive of lower survival during adulthood (25). The cumulative consequences of fear may thus be expected to not only include there being fewer offspring to begin with and some dying soon after (1, 9) but the survivors being permanently handicapped (15, 23, 24), reducing either their likelihood of surviving to adulthood (recruitment), or their fecundity or survival during adulthood (15, 25), the latter constituting transgenerational impacts (1, 13, 14).

Population growth is generally defined in relation to the number of breeding adults (26, 27). In most birds and mammals the two most critical determinants of the population growth rate (5, 28–30) are the number of young recruiting to the adult breeding population (additions) and breeding adult survival (losses). To experimentally test if fear itself can affect

**Significance**

Accurately evaluating the total impact of predators on prey population growth rates is fundamental to forecasting the consequences of predator conservation and management. That the fear (antipredator responses) predators inspire could contribute to this total impact has only relatively recently been recognized. We experimentally demonstrate that fear itself can impact prey population growth rates in free-living wildlife, extending to transgenerational impacts reducing population growth beyond the parental generation. We report how fear may contribute considerably to the total impact of predators and why this may be the norm in birds and mammals. The critical significance of our work lies in experimentally establishing that inferring the effects of predators using data on direct killing alone risks dramatically underestimating their total impact.

ECOLOGY

the population growth rate in free-living wildlife it is consequently critical to comprehensively quantify the effects on not just (i) fecundity and (ii) early offspring survival but also (iii) later offspring survival and (iv) breeding adult survival as well, to establish the cumulative impact on recruitment (i–iii), and whether recruitment is insufficient ($\lambda < 1$) or sufficient ($\lambda \geq 1$) to replace (iv) breeding adult losses (1, 10, 11, 31). Additionally quantifying if (v) recruits manifest evidence of reduced fecundity or survival during adulthood is critical to testing if the cumulative effects of fear extend to transgenerational impacts reducing population growth over generations (1, 13). The effects of fear on the survival of (iii) older offspring and (iv) breeding adults, and (v) offspring fecundity and survival during adulthood, remain experimentally untested in free-living wildlife, and this "dearth of evidence" is why the impact on population growth remains unknown (1, 11).

We exhaustively experimentally tested the impact of fear itself on the population growth rate over multiple generations in wild free-living song sparrows by manipulating fear over three annual breeding seasons and comprehensively quantifying the effects on all the components of population growth (i–iv) through to each subsequent season and then quantifying evidence of (v) transgenerational impacts in each subsequent season. We used a proven protocol to manipulate fear by intermittently broadcasting playbacks of predator (or nonpredator control) vocalizations at high but naturally occurring rates throughout the breeding season (1, 9) across multiple song sparrow territories at multiple sites ($n = 11$ to $15$) distributed among five small (< 200 ha) coastal islands in British Columbia, Canada (*SI Appendix*, Fig. S1), where they are year-round residents (9). In total, we quantified the effects on (i–iii) the recruitment of the offspring and (iv) the survival of breeding adults from 104 territories, 51 where predator playbacks were broadcast and 53 where nonpredators were. We employed daily nest checks and continuous video surveillance to determine (i) fecundity and (ii) the fate of every egg ($n = 564$) and nestling ($n = 507$) with certainty and further ensured egg and nestling fate was known with certainty by protecting every nest from predators of eggs and nestlings using seine netting and electric fencing (9). To quantify the effect of fear on the survival of (iii) older offspring we tracked the fate of 151 radio-tagged young from fledging to the end of the breeding season. All offspring ($n = 416$) and adults were fitted with individually colored leg bands, enabling us to quantify the effects of fear on (i–iii) recruitment and (iv) breeding adult survival, by resighting survivors during intensive surveys of each small island conducted in the year following each experimental year. To quantify evidence of (v) transgenerational impacts we recorded the number of songs sung by recruits ($n = 24$), knowing this is predictive of survival during adulthood (25). Finally, to verify their external validity we compared the effect sizes demonstrated in our experiment with those reported in observational studies concerning purported fear effects (1) and comprehensive reviews of predator manipulation experiments involving free-living birds and mammals (7, 8).

## Results and Discussion

Fear itself significantly reduced the population growth rate; the mean $\lambda$ for the predator playback treatment (mean $\lambda = 0.91$, 95% CI = 0.80 to 1.04) and that for the nonpredator (control) treatment (mean $\lambda = 1.06$, 95% CI = 0.96 to 1.16) each being outside the 95% CIs concerning the other. This resulted because fear itself had cumulative, compounding adverse effects (Fig. 1A and Table 1), causing the number of young recruiting to the adult breeding population (i–iii) to be reduced by more than half (53% fewer recruits were produced by adults that heard predator playbacks; *SI Appendix*, Table S1), which was insufficient to replace (iv) breeding adult losses ($\lambda = 0.91$), with the consequence that the fear-induced reduction in the
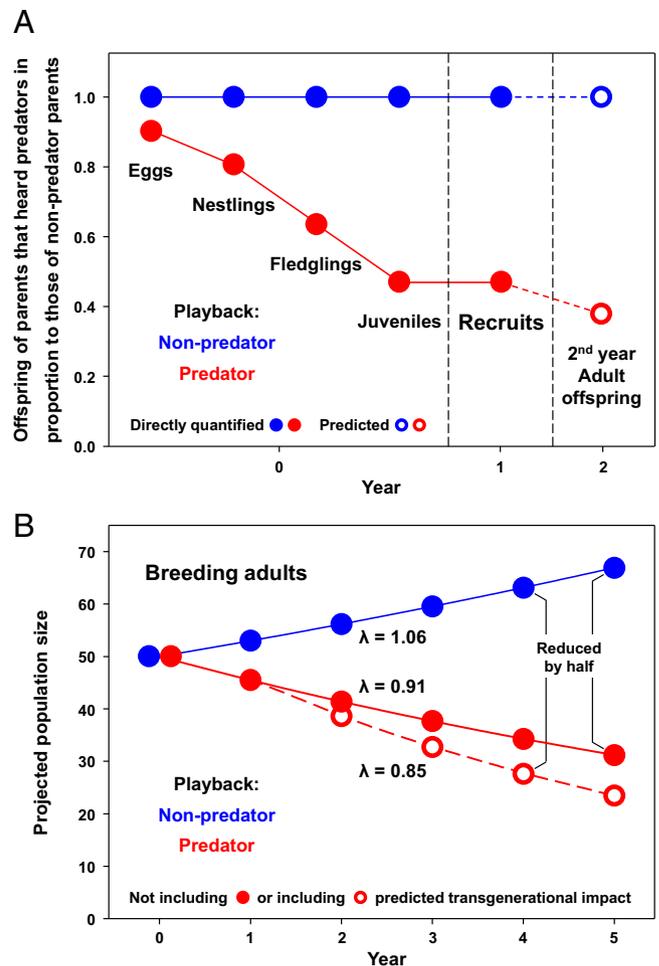


**Fig. 1.** Impact of fear itself on components of the population growth rate ($\lambda$) and projected population size. (*A*) Directly quantified, cumulative, compounding adverse effects of fear on fecundity and offspring survival to recruitment (solid circles) and the predicted additional transgenerational impact of fear on offspring survival as adults (open circles), illustrated by plotting offspring number in the predator (red) playback treatment as a proportion of those in the nonpredator (blue) treatment, at each life-history stage. (*B*) Population size in the predator (red) and nonpredator (blue) playback treatments projected over 5 years, calculating $\lambda$ using just directly quantified components (solid circles) and additionally including the predicted transgenerational impact of fear on offspring survival as adults (open circles).

population growth rate was projected to halve the population size relative to controls in just 5 years (Fig. 1B). Control adults that heard nonpredator playbacks produced slightly more recruits than needed to replace losses among them ($\lambda = 1.06$), and their numbers were thus projected to moderately increase (Fig. 1B). There was significant evidence that the cumulative adverse effects of fear extended to include a (v) transgenerational impact reducing the survival of offspring during adulthood (Fig. 1A and Table 1), and accounting for this even greater total impact of fear over generations, the fear-induced reduction in the population growth rate ($\lambda = 0.85$) was projected to halve the population in just 4 years (Fig. 1B).

The cumulative, compounding adverse impacts of fear on recruitment (i–iii) resulted because, compared to control females that heard nonpredator playbacks, females that heard predators (i) laid 10% fewer eggs, (ii) 11% fewer of their eggs survived to hatching, (ii) 21% fewer of their nestlings survived to fledging, and (iii) 26% fewer of their fledglings survived as

**Table 1. Effects of playback treatment on all the components of population growth (i–iv) and evidence predictive of a (v) transgenerational impact**

| Population growth component* | Directly quantified measure | Predator X̄ or N | Predator SE | Nonpredator X̄ or N | Nonpredator SE | Statistic | P |
|---|---|---|---|---|---|---|---|
| (i) | Eggs laid (clutch size) | 3.21 | 0.09 | 3.55 | 0.09 | $F_{1,78} = 8.0$ | 0.006 |
| (ii) | Egg survival | 0.84 | 0.03 | 0.94 | 0.03 | $F_{1,79} = 5.2$ | 0.025 |
| (ii) | Nestling survival | 0.69 | 0.03 | 0.88 | 0.02 | Wald $\chi^2 = 6.7$ | 0.003 |
| (iii) | Fledgling survival | 0.46 | 0.06 | 0.62 | 0.06 | Wald $\chi^2 = 6.4$ | 0.006 |
| (i–iii) | Resighted recruits | 15 | | 32 | | $\chi^2_1 = 5.5$ | 0.019 |
| (iv) | Adult survival | 0.49 | 0.06 | 0.57 | 0.07 | Wald $\chi^2 = 0.8$ | 0.380 |
| (v) | Recruit song number† | 7.00 | 0.47 | 8.75 | 0.33 | $F_{1,20} = 7.0$ | 0.007 |

*See main text for definitions.
†Predictive of a transgenerational impact on offspring survival during adulthood (see main text).

juveniles at the end of the breeding season (Fig. 1A, Table 1, and *SI Appendix*, Table S1). Multiplying the known number of eggs laid (i) by each exhaustively quantified known-fate measure of offspring survival (ii–iii), by the end of the breeding season predator playback parents had on average produced 53% fewer juveniles than control parents (Table 1 and *SI Appendix, Table S1*). This average of 53% fewer predator playback juveniles directly corresponds to the 53% fewer predator playback recruits resighted in the subsequent season (Table 1 and *SI Appendix, Table S1*), demonstrating that the cumulative impacts of fear on juvenile numbers carried straight through to impact recruitment (i–iii) without any abatement (Fig. 1A). The number of directly resighted recruits differed significantly from that expected if each of the 51 pairs of predator playback parents and 53 pairs of control parents produced an equal number of recruits (Table 1). This result demonstrates the effect of fear in reducing recruitment (i–iii), and our comprehensive quantification of the impacts on each component reveals how (i, ii, and iii; Table 1). Fear did not significantly affect (iv) breeding adult survival (Table 1). Consequently, it was the fear-induced 53% reduction in recruitment that caused there to be insufficient recruits to replace breeding adult losses ($\lambda = 0.91$), thereby producing the projected decline in population size (Fig. 1B).

Fear itself demonstrably permanently handicapped surviving offspring, significantly reducing the song number sung by recruits (Table 1), which from the known relationship between song repertoire size and adult survival in song sparrows (25) was predictive of a (v) transgenerational impact entailing 18% lower survival during adulthood among the offspring of parents that heard predators (Fig. 1A). Accounting for this evidence of a transgenerational impact the population growth rate was projected to be further reduced ($\lambda = 0.85$) in the second and subsequent years after the year in which these offspring were reared (Fig. 1B). This demonstrated permanent handicapping of offspring was entirely consistent with our prior research regarding impaired brain development (23, 24), because there was abundant evidence of early developmental stress resulting from fear-induced reductions in parental investment and care. All of the impacts of fear on offspring survival (ii and iii; Table 1) occurred during the period of parental care, including the impact on fledgling survival (iii), which occurred in the first 7 d after fledging (*SI Appendix*, Fig. S2, lines 419–434), when fledglings are still dependent on parental provisioning (22). Parents that heard predators provisioned their offspring significantly less often (9, 22), and their offspring were correspondingly significantly hungrier and had significantly less fat both as nestlings and as dependent fledglings (*SI Appendix*, lines 435–450). Finally, our prior research regarding impaired brain development demonstrated comparable negative effects of early developmental stress on brain development in both males and

females (23), pointing to comparable adverse effects on the survival of both sexes during adulthood.

The significant impacts of fear demonstrated in our experiment (Table 1) were all robust and reproducible, evidenced by there being no significant treatment-by-year interactions over the 3 years in which the experiment was repeated (all $P > 0.366$; *SI Appendix*, Table S2). Experiments enable strong inference concerning causation but they must also have external validity, corroborated by demonstrating effect sizes corresponding to observational studies. Our methodology and the magnitudes of the effect sizes demonstrated in our experiment correspond closely with reported levels of natural variation. Predator (and nonpredator) vocalizations were broadcast at a rate (9.3 min/h) comparable to naturally occurring predator vocalizations (9.5 min/h) recorded at naturally high predation risk sites in a study regarding the effects of natural variation in predation risk on fecundity and facets of offspring survival in 10 species of songbirds (20). The size of the effect on (i) fecundity in our experiment (−0.10, Table 1; calculated as $\ln[\bar{X}_{treatment}/\bar{X}_{control}]$ following ref. 8) was almost identical to that in a study of song sparrows (−0.09) contrasting naturally high versus low predation risk sites (32) and was identical to the mean effect size (−0.10) reported in the just-mentioned study on 10 species of songbirds (20). Similarly, the effect size regarding (ii) egg survival (−0.11) was comparable to that in response to natural variation in predation risk in song sparrows [−0.12 (33)] and the mean effect size in the study on 10 songbird species [−0.22 (20)], and the same was true of the magnitude of the effect on (ii) nestling survival (−0.24, −0.20, and −0.28; this study and refs. 33 and 20, respectively). Likewise, the effect on (iii) the survival of older offspring (−0.30) well accords with that (−0.27) reported as resulting from natural variation in parental fearfulness in song sparrows (22).

The generality of our results is strongly supported by the impacts all being attributable to fear-induced reductions in parental investment and care (refs. 9, 18, 19, and 22 and *SI Appendix*), because abundant evidence indicates such impacts may be almost universal in birds and mammals (1, 22). Parental care is a fundamental characteristic of most birds and all mammals (34), fear has been shown to impair parental investment and care in diverse birds and mammals (1, 35–41), reduced care consistently results in poorer offspring condition and consequent lower survival (15, 30), and there is correspondingly a growing body of experimental and observational research documenting resulting reductions in fecundity and offspring survival in free-living birds and mammals, comparable to those demonstrated in our experiment (1, 16, 17, 20, 21, 42, 43). Numerous studies have shown that one of the principal and almost universal costs prey incur in attempting to avoid being killed is reduced food intake due to increased vigilance or avoidance of predators (1–3, 6, 10, 11). In species in which longevity is

Allen et al.
Fear of predators in free-living wildlife reduces population growth over generations

PNAS | 3 of 6
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ECOLOGY

correlated with lifetime reproductive success, as in most birds and mammals (28–30), to ensure their own survival parents can be expected to transfer the costs of their antipredator responses to their offspring (e.g., by provisioning them less), because while this may reduce current reproductive success it provides the surest means of achieving higher lifetime reproductive success (1–3, 6, 22, 28–30, 35–40). Fear effects on adult survival are consequently not anticipated to be common, and our not finding a significant effect on adult survival (Table 1) is thus entirely consistent with general life-history expectations concerning birds and mammals (1).

Species vary in the strength of their antipredator responses and there is correspondingly well-documented variation among species in the strength of the purported effects of fear on fecundity and offspring survival in free-living wildlife (1, 11, 16–22, 32, 33, 35–45). Within the context of this known variation the antipredator responses we recorded are common among birds and mammals, and the magnitudes of the effects of fear on the components of population growth we report (Table 1) are all near the midpoints of the documented variation among species, as we have discussed. There is thus nothing unusual about the responses and effects we demonstrate. An influential recent review (11) meticulously detailed all of the many reasons why an effect of fear on population growth cannot simply be inferred to result from an effect on any one component of population growth, or even two or three, because of the possible existence of "doomed surpluses," for example. What must be demonstrated is that the effects on the components all link together to cause a net effect on population growth (1, 10, 11). This review identified that this has not been accomplished in any free-living wild animal in any taxon, let alone birds or mammals, and other recent reviews corroborate this "dearth (i.e., absence) of evidence" (1, 10, 11). Rather than the types of responses or magnitudes of effects on individual components, what is thus unique about our study is our comprehensive quantification of the effects of fear on all the components of population growth and our experimental demonstration that these effects can all link together to significantly reduce the population growth rate in free-living wild prey (1, 10, 11).

That predators are more than merely scavengers (12) that can and do affect prey population growth rates in free-living wild birds and mammals was eventually shown to be compellingly well-established in two comprehensive reviews of 223 experiments involving the addition or removal of predators, both published in 2010 (7, 8). Adding or removing predators demonstrates their total impact on prey populations, that is, the combined impacts of direct killing and fear [the costs prey incur in attempting to avoid being killed (1, 4, 6, 8)]. These reviews reported a mean effect size of 0.68 regarding the total impact on reproductive responses [e.g., mean recruitment (8)] and a mean effect size of 0.11 pertaining to the total impact on population growth rates (7). These mean effect sizes correspond closely with the absolute values of the effect sizes demonstrated in our experiment concerning the impacts of fear on recruitment (0.76; Table 1) and the population growth rate (0.15; Fig. 1B). Consequently, our results not only demonstrate that fear itself can significantly impact prey population growth rates in free-living wildlife but also that this may constitute a very considerable part of the total impact of predators. The critical significance of this is that it experimentally establishes that attempting to utilize data on direct killing alone to infer the effects of predators risks dramatically underestimating the total impact predators have on prey populations (1–3, 6, 8–11).

## Conclusions

The past decade has seen a "paradigm shift in ecology" reappraising the importance of predators in wildlife population, community, and ecosystem dynamics (1, 46–48). Progress has recently been made in experimentally demonstrating the community-level impacts fear of predators can have in wildlife systems (1), which has drawn attention to the contrasting "dearth (absence) of evidence" concerning the impact on population growth (1, 10, 11). Critically, this dearth does not concern the various components, such as fear effects on parental care, fecundity, or offspring survival, for which there is an abundance of evidence (1, 9, 35–41), but rather the absence of demonstrations that these components do all link together to affect prey population growth (1, 10, 11). The significance of our eliminating this absence by experimentally demonstrating that these components can all link together and that fear itself can impact prey population growth rates in free-living wildlife is that it verifies that, from the commonality of the components, fear effects on prey population growth rates, while not necessarily universal, can be anticipated to be commonplace (1–3, 6, 8–11). As our results illustrate, even if the effects of fear on individual components are modest, if they are cumulative and compounding the total impact of fear on the prey's population growth rate can be very considerable.

## Materials and Methods

**Experimental Design, Sites, and Field Procedures.** Results regarding the effects of fear on (i) fecundity and (ii) early offspring survival in the first year were published previously (9), and exhaustive details concerning the experimental design, sites, and field procedures can be found therein and in the *SI Appendix*. Briefly, playbacks were broadcast from 15 March to the end of July, composed of the vocalizations of eight species of locally present predators, or eight nonpredators, played at appropriate periods in the diel cycle, with overall matching acoustic and frequency characteristics (*SI Appendix*, lines 197–258). The eight species of predators comprised the Common Raven (*Corvus corax*), Northwestern Crow (*Corvus caurinus*), Cooper's Hawk (*Accipiter cooperii*), Brown-headed Cowbird (*Molothrus ater*), raccoon (*Procyon lotor*), Barred Owl (*Strix varia*), Western Screech-Owl (*Otus kennicotti*), and Northern Saw-whet Owl (*Aegolius arcadius*). The eight nonpredator species, here listed in the order matching the corresponding predator, comprised the Canada Goose (*Branta canadensis*), Mallard Duck (*Anas platyrhynchos*), Northern Flicker (*Colaptes auratus*), Rufous Hummingbird (*Selasphorus rufus*), harbor seal (*Phoca vitulina*), wood frog (*Rana sylvatica*), Common Loon (*Gavia immer*), and Pacific chorus frog (*Pseudacris regilla*). All of the predators are known to kill adult song sparrows or their offspring (*SI Appendix*, lines 182–196). To avoid habituation we used an average of eight exemplars of each species' vocalizations, vocalizations varied in duration and were played randomly, and speakers were repositioned several meters every eighth day. Predator and nonpredator playbacks were broadcast at separate sites, each with one to four song sparrow territories (*SI Appendix*, Fig. S1 and lines 152–170). All sites lay within a 2.7-km radius centered at 48° 44.35′ N and 123° 23.27′ W. Predator and nonpredator playback sites were paired on each small island within 500 m of one another. Every eighth day 100-m transects were walked at each site verifying that there were no significant differences between predator and nonpredator playback sites in the frequency or number of actual predators seen or heard (*SI Appendix*, lines 235–240).

Egg number and the known-fate survival of eggs, nestlings, and fledglings (Table 1) were all determined with certainty through a combination of daily nest checks, continuous video surveillance and protecting nests from predators of eggs and nestlings while young were in the nest (9), and tracking and visually resighting radio-tagged young every second day after they left the nest, to the time they died or the end of the breeding season (31 August; *SI Appendix*, lines 259–309). Young were radio-tagged while in the nest to ensure we accurately quantified survival immediately following fledging, when mortalities are typically most frequent (49, 50). Protecting nests from predators of eggs and nestlings (primarily Ravens, Crows, and raccoons; *SI Appendix*, lines 186–188) helped establish egg and nestling fate with certainty but potentially caused us to underestimate the adverse effects of fear, because a previous experiment on song sparrows at these same sites demonstrated that losing a nest to a predator causes breeding females to become more fearful and subsequently lay smaller clutches (1, 18). Critically, parents were in no way at any time protected from their predators and the actual risk of predation to parents was thus entirely natural, as recommended by the aforementioned influential recent review concerning accurately quantifying the impacts of fear on prey population size (11).

To resight recruits and adults in the year following each experimental year, beginning in early March, immediately before the breeding season, at least two exhaustive intensive surveys were conducted of each small island by traversing each island along transects spaced 50 m apart (less than the average 70-m width of a song sparrow territory; ref. 9), and at every 50 m along each transect, broadcasting playbacks of song sparrows singing, which reliably attracts any song sparrow in the area (33). Multiple lines of evidence indicate that detectability was close to or actually 100% (*SI Appendix*, lines 310–327). Additionally, whereas differential detectability (or differential emigration) between the treatments might otherwise be invoked as alternative explanations of differences between the treatments in the apparent survival of recruits or adults, there was no (recruits) or little (adults) difference in resighting to explain. The ratio of predator to nonpredator playback juveniles was identical to the ratio of predator to nonpredator playback recruits (Fig. 1A), i. e., apparent offspring survival from the end of the breeding season to recruitment was identical in both treatments (= 0.17; see below and *SI Appendix*, lines 328–341), and there was similarly no substantive difference in apparent adult survival (Table 1).

When recruits were resighted we recorded their song repertoire size following published procedures (24, 25), described in detail in the *SI Appendix* (lines 356–358). To predict the transgenerational impact of fear on the survival of recruits as adults we used the relationship between survival (longevity) and song number detailed in ref. 25 (*SI Appendix*, lines 342–362): longevity (years) = (song repertoire size × 0.36) + 0.42. As already observed, our prior research demonstrating that early developmental stress impairs brain development in both males and females (23) points to comparable adverse effects on the survival of both sexes during adulthood. Importantly, if one sex were more adversely affected and consequently had lower survival during adulthood than the other, because biparental care is effectively obligatory in song sparrows (*SI Appendix*, lines 175–178), the effect on population growth would be projected to reflect the impact on the more affected (and consequently more limited) sex (26).

**Population Growth Rate (λ).** We used stage-structured Leslie Matrix models to calculate the population growth rate (λ) for each treatment (31). Our Leslie Matrices corresponded with the directly quantified components of population growth delineated in Table 1, beginning with fecundity (eggs laid), followed by five survival stages: egg survival, nestling survival, fledgling survival, survival from the end of the breeding season to recruitment, and adult survival. Survival from the end of the breeding season to recruitment was determined by dividing the number of directly resighted recruits (Table 1) by the calculated number of juveniles at the end of breeding (eggs laid × egg, nestling, and fledgling survival; *SI Appendix*, lines 328–341), giving a value of 0.17 for each treatment. To determine the 95% CI concerning λ for each treatment we used the recommended bootstrap method (31, 51, 52), conducting 10,000 iterations of stochastic Leslie Matrix models using the means and variation of the population growth components delineated in Table 1. Where comparisons are made between two treatments (populations) with equivalent sample sizes, as in our case, results using the bootstrap are robust to heterogeneity of variances (52). To calculate λ accounting for the evidence of a transgenerational impact of fear, we first input the demonstrated effect of fear on recruit song number (Table 1) into the equation described in the previous paragraph to produce the prediction that predator playback recruits would have 18% lower adult survival than their parents in the initial cohort (0.40 vs. 0.49), and we then iterated this difference in survival between cohorts over a projected 5-year period to determine the mean effect on population growth (λ = 0.85).

**Statistical Analyses.** With regard to the components of population growth reported in Table 1, fecundity (eggs laid) and egg survival (the proportion of eggs that hatched) were analyzed using three-factor general linear mixed-model ANOVAs (GLMMs), and nestling survival and fledgling survival were analyzed using Cox-proportional hazards models. The independent variables in these analyses were playback treatment, year, and nest number (one or two), with parental identity included as a random effect. The effect of fear in reducing the number of directly resighted recruits was tested using a $\chi^2$ test as described in the *Results and Discussion*. Apparent adult survival from one year to the next was analyzed using a generalized estimating equation (GEE) with a binomial distribution (alive or dead) and logit-link function, the fixed factors being playback treatment and year, with identity included as a random effect to account for individuals resighted in more than 2 years. Recruit song number was analyzed using a two-factor ANOVA with playback treatment and year as independent variables, there being no correlated data requiring random effects. Additional details concerning the statistical analyses are reported in the *SI Appendix* (lines 393–417), along with complete model results (*SI Appendix*, Table S2).

**Data Availability.** Data have been deposited in a publicly accessible, permanently archived, institutional repository at Western University (https://ir.lib.uwo.ca/biologypub/115).

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Allen et al.
Fear of predators in free-living wildlife reduces population growth over generations

PNAS | 5 of 6
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ECOLOGY

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