

Correction

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Correction for “Chronic anthropogenic noise disrupts glucocorticoid signaling and has multiple effects on fitness in an avian community,” by Nathan J. Kleist, Robert P. Guralnick, Alexander Cruz, Christopher A. Lowry, and Clinton D. Francis, which was first published January 8, 2018; 10.1073/pnas.1709200115 (*Proc Natl Acad Sci USA* 115:E648–E657).

The authors note that on page E651, left column, first full paragraph, line 14, “reviewed in ref. 26” should instead appear as “reviewed in ref. 25.”

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Chronic anthropogenic noise disrupts glucocorticoid signaling and has multiple effects on fitness in an avian community

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Anthropogenic noise is a pervasive pollutant that decreases environmental quality by disrupting a suite of behaviors vital to perception and communication. However, even within populations of noise-sensitive species, individuals still select breeding sites located within areas exposed to high noise levels, with largely unknown physiological and fitness consequences. We use a study system in the natural gas fields of northern New Mexico to test the prediction that exposure to noise causes glucocorticoid-signaling dysfunction and decreases fitness in a community of secondary cavity-nesting birds. In accordance with these predictions, and across all species, we find strong support for noise exposure decreasing baseline corticosterone in adults and nestlings and, conversely, increasing acute stressor-induced corticosterone in nestlings. We also document fitness consequences with increased noise in the form of reduced hatching success in the western bluebird (*Sialia mexicana*), the species most likely to nest in noisiest environments. Nestlings of all three species exhibited accelerated growth of both feathers and body size at intermediate noise amplitudes compared with lower or higher amplitudes. Our results are consistent with recent experimental laboratory studies and show that noise functions as a chronic, inescapable stressor. Anthropogenic noise likely impairs environmental risk perception by species relying on acoustic cues and ultimately leads to impacts on fitness. Our work, when taken together with recent efforts to document noise across the landscape, implies potential widespread, noise-induced chronic stress coupled with reduced fitness for many species reliant on acoustic cues.

acoustic environment | anthropogenic noise | birds | stress response | perceived predation risk

Human-made noise is a widespread and complex stimulus that alters habitats, degrades natural acoustic conditions, and partially or fully excludes species that are sensitive to noise exposure from affected areas (1–4). The exact mechanisms by which noise disrupts animals and their environments are still debated, but recent work links noise exposure with alterations in vocalization, vigilance, foraging, and parental behavior (5–12). Despite this recent progress, key questions remain unanswered, especially whether anthropogenic noise represents a chronic stressor for free-living animals and the severity of any resulting fitness effects from noise or noise-induced stress. Although not unexplored (13–20), the effect of noise on stress and fitness is complex (21). The identification of mechanisms is especially difficult given the possibility that noise could elicit a stress response directly through extreme exposure (22, 23) or indirectly by altering the interaction between animals and their environment (13). Noise levels in wild systems reach the extreme amplitudes that are observed to directly elicit stress responses in laboratory studies [i.e., 90–105 dB (23); 130 dB (24)] only at very close proximity to noise sources. At lower exposure levels, anthropogenic noise is more likely to elicit stress responses indirectly by increasing the difficulty of coping with

external challenges (e.g., territory defense) or by creating anxiety through reduced detectability and predictability of threats (e.g., acoustic masking of predator alarm sounds) (8, 24–26), or both. Clarifying the potential impacts of chronic noise exposure in wildlife is timely and needed, given the nearly ubiquitous presence of anthropogenic noise worldwide and the forecasted global rise in noise-producing infrastructure (1).

Conservation physiologists often use measurements of an organism’s baseline circulating stress hormones, or glucocorticoids (GCs), as an indirect measure of habitat quality and a proxy measure for potential fitness (27). GCs are secreted from the adrenal gland in a coping response to challenge and are the result of activation of the hypothalamic–pituitary–adrenal (HPA) axis, a chemical cascade triggered by neuronal signals sent from hierarchical neural systems to the hypothalamus in response to the brain’s perception of a stressor (28, 29). The HPA axis is a highly conserved vertebrate stress system activated during allostasis, the process by which animals maintain stability, or homeostasis, through change (30). While GCs are modulated in ultradian, circadian, and seasonal rhythms to meet challenges related to predictable energy deficits, frequent disturbance from chronic stressors encountered in low-quality habitats can push an

Significance

Studies examining relationships among habitat disturbance, physiology, and fitness in wild animals often produce contradictory or inconclusive results, casting doubt on current conservation physiology predictive frameworks linking stress and fitness. We apply a new framework drawn from experimental systems utilizing chronic inescapable stressors to explore how noise, an environmental stimulus common to wildlife habitats worldwide, disrupts stress hormone signaling and impacts fitness. We utilize a natural experiment to show that chronic, anthropogenic noise reduced baseline corticosterone levels, increased acute corticosterone response, and, at highest amplitudes, negatively impacted multiple measures of fitness across three species of birds. Our work brings conservation physiology theory involving wild animals into needed alignment with recent theories based on chronic stress in laboratory studies.

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organism's physiological state out of the range of a normal allostasis and into a state of allostatic overload. Overload states are often pathological and have been shown to have fitness consequences (30, 31). Although increased allostatic load may suggest higher baseline GCs, the empirical data have been equivocal at best; different studies find decreased as well as increased GCs in response to chronic stressors (17, 25, 32–36).

Baseline corticosterone (hereafter, “cort”) levels are generally predicted to positively associate with the intensity of habitat disturbance in what has been dubbed the “cort-fitness hypothesis” (21, 27). In contrast to the predictions of this hypothesis, results from laboratory and human systems suggest that exposure to chronic stressors is often associated with decreased basal GC levels, hypocorticism, and GC insensitivity (37, 38). The development of hypocorticism could be a coping mechanism that saves an organism from experiencing the severe effects of allostatic overload (39), but there is evidence that it can lead to reduced fitness. For example, a laboratory-based system using mice shows how chronic subordinate social rank triggers hypocorticism, reflected by reduced basal GC levels and GC insensitivity that can be accompanied by an inflammatory response (25, 40) and reduced weight gain (41). Unlike situations in which animals fail to react to repeated chronic stressors, physiological results in this laboratory system are paired with negative fitness outcomes, suggesting that animals do not habituate (42). Additionally, these studies show that individuals experiencing hypocorticism can develop HPA-axis sensitivity to heterotypic stressors, leading to increased GC responsiveness following experimental acute stress events (25, 43). In natural systems, such heterotypic stressors could include predation attempts, competitor interactions, or confrontations with humans and other anthropogenic disturbances. While much work has focused on human and rodent laboratory models, the sensory blanketing of the acoustic environment by chronic anthropogenic noise provides a unique opportunity to test if a chronic, inescapable stressor can cause similar stress and fitness responses in wild animals.

The impact of noise is thought to be most severe when frequencies overlap auditory environmental cues, a phenomenon

known as “acoustic masking,” which leads to reduced detection and discrimination of key acoustic signals and cues. Acoustic signals and cues from both conspecifics and heterospecifics provide important information about the immediate environment, including the quality and location of competitors (44) and the presence or absence of predators through alarm or nonalarm vocalizations and adventitious sounds (45–49). Given the capacity for chronic noise to consistently mask biologically relevant cues (8, 26, 47, 50), animals living in areas with high levels of noise may fail to receive information about their local habitats, leading to a continual state of perceived unpredictability and reduced security (44, 47, 51). The experience of constant environmental uncertainty among both parents and nestlings, whether justified or not (24), could cause chronic activation of the HPA axis and affect both GCs and fitness through reduced hatching success of eggs and provisioning of young (52).

To date, no studies have simultaneously examined relationships among noise, GCs, and fitness in animals that settle and breed in natural areas exposed to chronic anthropogenic noise. To address this significant gap and provide a needed conceptual alignment of recent work in conservation physiology with related work on chronic stress, we performed a natural experiment using wildlands in northern New Mexico's San Juan Basin, where a community of birds breeds along a gradient of noise produced by natural resources extraction (Fig. 1). We measured noise levels, cort, and fitness-relevant variables, e.g., hatching success and nestling body condition, in populations of three species of cavity-nesting birds with different tolerances to noise: western and mountain bluebirds (*Sialia mexicana* and *Sialia currucooides*, respectively), and ash-throated flycatchers (*Myiarchus cinerascens*) (53). We predict that long-term exposure to continuous anthropogenic noise will act as a chronic stressor, disrupting GC signaling in adults and nestlings, with the greatest impact at sites with highest amplitude noise. We also predict that long-term exposure to continuous anthropogenic noise will be linked to reduced fitness. Incorporating multiple species and disturbance (53–57) into a multiyear study defined by a chronic, homotypic stressor represents the most highly integrated study of the effects of anthropogenic noise on wild birds to date.

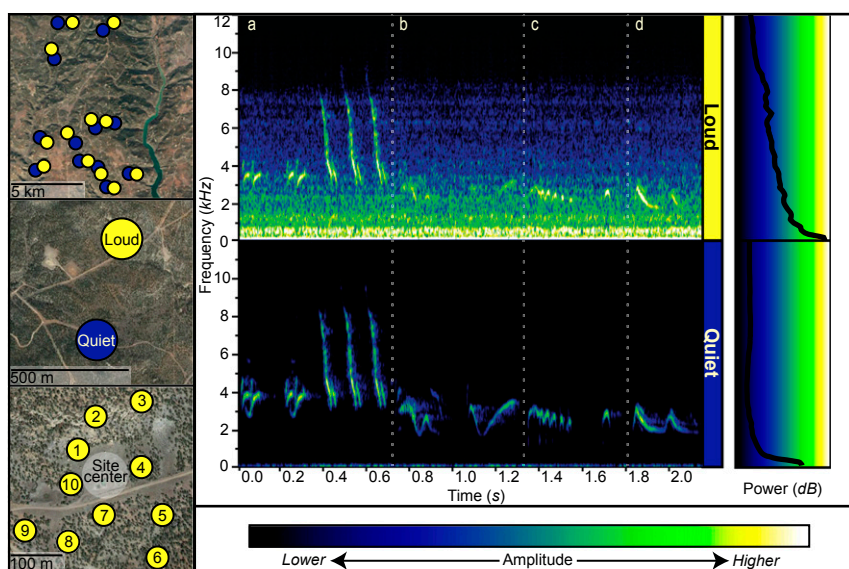


Fig. 1. This conceptual figure shows the study system design and the acoustic properties of sites with and without compressor noise. (Left) The three nested spatial scales included in the study: the full system (Top), loud and quiet pairs (Middle), and individual sites (Bottom). The Bottom shows nest boxes (labeled 1–10) arrayed around the site center, which was the centroid location of a well pad. (Center) A spectrogram of recorded background noise at a louder area (Upper) and quieter area (Lower). The songs of four common species that are found in RCHMA, including representatives from this study are included to depict the masking potential of noise: (a) spotted towhee; (b) plumbeous vireo; (c) ash-throated flycatcher; and (d) western bluebird. (Right) Power spectra that show the amplitude or “power” of compressor noise at frequencies between 0 and 12 kHz.

Table 1. Effects of noise and other variables on cort and fitness

Dependent variable	N	Fixed effects	Random effects	k	R ²	AIC _c	Null AIC _c	χ ²
Cort predicted by noise								
Adult baseline cort	65	Noise*– Species*	Site Nest ID	8	0.592	369.801	381.857	<0.001
Nestling baseline cort	162	Life stage* Noise*– Species*	Year	6	0.319	978.299	1,030.426	<0.001
Nestling acute stressor-induced cort	161	Noise*+ Species* Chicks*+ Time*– Tree cover*+	Nest ID	9	0.766	1,134.000	1,202.198	<0.001
Fitness predicted by noise								
All species hatch success	364	Intercept	None	1	0	218.722	Na	Na
Western bluebird hatch success	133	Noise*– Tree cover*+	None	3	0.039	89.489	91.538	0.045
Ash-throated flycatcher hatch success	138	Noise*+	Year	3	0.024	75.027	75.280	0.126
Mountain bluebird hatch success	93	Intercept	None	1	0	56.586	Na	Na
Nestling feather growth (PC1)	272	Noise _{quad} * Species*	Year Nest box Nest ID	9	0.907	295.644	353.080	<0.001
Nestling body size (PC2)	272	Noise _{quad} * Species* Chicks*– Distance*– Lay date*–	Nest ID	10	0.739	309.872	364.547	<0.001

All models presented are best-performing models. The term for life stage is included as the effect of the provisioning stage on the dependent variable. The term “distance” refers to the distance in meters from the nest box to the well pad center or compressor station. Models that do not include random effects were run as GLMMs following our described methods. k, parameters estimated; Na, not applicable.

*Predictors that do not include zero in their 85% confidence limits; all continuous predictors are marked with the direction of their effect on the dependent variable.

hearing birdsong could be used as a safety signal in birds, and continual masking could chronically impair risk perception, leading to environmental uncertainty and activation of the stress response. While birds are away from the nest on foraging trips, noise throughout the territory (53) could decrease hunting efficiency (7, 50), reducing energy intake and leading to increased allostatic load relative to individuals in quieter territories. Unlike adults, nestlings are incapable of escaping nest boxes and are constantly exposed to noise. This chronic, inescapable disturbance could stimulate stress and hypocorticism in nestlings through reduced reception of heterospecific (48) or parental (64) cues. Alternatively, the effect of compressor noise on parental vocal behavior (65) could interact with the effects of masking and lead to reduced detectability and increased uncertainty about environmental risk. Provisioning behavior could also be negatively affected by noise, leading to increased allostatic load in nestlings, discussed more below.

We also tested if, as in other systems, responses to acute stressors in animals under chronic stress were higher when exposed to heterotypic stressors. We measured cort levels in nestlings 10 min after capture and fit models similar to those for baseline measurements. The model with a common effect for noise but with species-specific differences best explained acute stressor-induced cort levels in nestlings. In contrast to baseline cort results, the effect of noise on acute stressor-induced cort was positive (LMM, Gaussian distribution, $\beta_{\text{noise}} = 1.297$, 85% CI: 0.067–2.538) (Fig. 2 and Table 1). The finding of suppressed baseline cort and increased acute stress-induced cort is consistent with many laboratory studies on model species, which suggest that hypocorticism results from chronic psychological stress (reviewed in ref. 26). Sensitization of cort response to acute stressors following exposure to a chronic stressor has also been found in nestling European starlings exposed to a chronic psychological stress protocol (32) but not in wild-caught adult birds exposed to a similar treatment in a laboratory setting (33). This

response could be adaptive in nestlings experiencing increased perceived predation risk, as a heightened reactivity during this stage could prime them for more efficient escape effort (66). However, early fledging might trade off with the accumulation of body mass, which can reduce the probability of postfledging survival (67–69). Although hypocorticism has been proposed as a protective response to increased allostatic load that might allow affected individuals to avoid the most serious effects of overload states (39), the attenuation of baseline cort is also potentially harmful and has been associated with inflammation, disease susceptibility (25), anxiety (43), and reduced exploration of novel objects (70). Thus, studies that explore hormone signaling and survivorship of individuals are necessary to fully quantify the costs of these responses to noise.

Effect of Noise on Fitness: Hatching Success. We found that a summary model including all species yielded uninformative results, and we therefore present species-specific models for hatching success (Table 1). Results from these models suggest that hatching success was significantly affected by noise in one species, the noise-tolerant western bluebird (53). In support of our prediction that increased noise would lead to decreased fitness, hatching success in the western bluebird was negatively associated with noise levels at the nest box [generalized linear mixed-effect model (GLMM), binomial distribution, $\beta_{\text{noise}} = -0.483$, 85% CI: -0.892 to -0.075] (Fig. 3 and Table 1). Egg-hatching rates in ash-throated flycatchers showed a weak, positive relationship with noise (GLMM, binomial distribution, $\beta_{\text{noise}} = 0.658$, 85% CI: 0.036–1.376) (Table 1), but this model was indistinguishable from the null hypothesis [change in corrected Akaike information criterion (ΔAIC_c) = 0.25]. Similarly, there was no clear effect of noise on hatching rates in mountain bluebirds. Overall, results from all three species may be best explained by previously described nesting patterns.

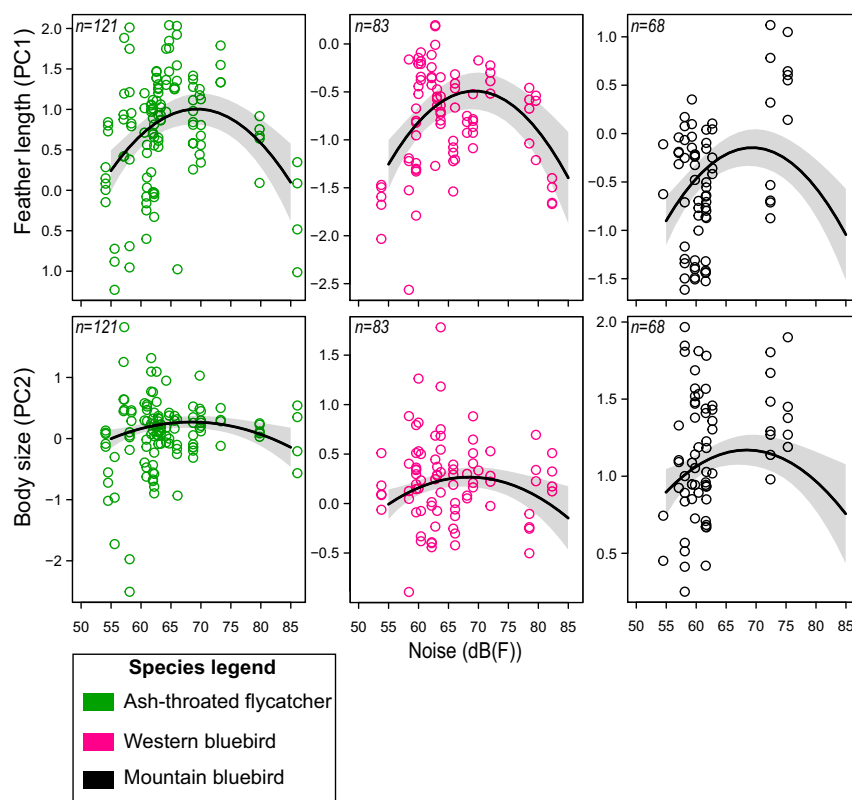


Fig. 4. The relationship between noise exposure and nestling development, represented by principal components axes, in all three species. Noise exposure had a nonlinear effect on feather development (*Upper Row*) and body size (*Lower Row*) in nestlings that was supported across species. The gray-shaded areas indicate the 85% confidence intervals for each estimated effect.

analogous to actual high predation risk, leading to increased vigilance or distraction but with no mechanism for escape.

Effect of Cort on Fitness. Surprisingly, there was no relationship between nestling baseline or acute stressor-induced cort on either nestling body condition PC axis. Instead, maternal baseline cort levels had strong influences on body condition, but with stage- and species-specific variation. For example, during provisioning, the relationship between adult female baseline cort and nestling body condition is species specific. Maternal baseline cort had a negative effect on nestling PC_{feather} in ash-throated flycatchers (LMM, Gaussian distribution, $\beta_{\text{cort}} = -0.257$, 85% CI: -0.363 to -0.150) (Table 2) and a positive effect in western bluebirds (LMM, Gaussian distribution, $\beta_{\text{cort}} = 0.900$, 85% CI: 0.673 – 1.124 ; Table 2). Adult female baseline cort levels were negatively associated with nestling PC_{size} in provisioning western bluebirds (LMM, Gaussian distribution, $\beta_{\text{cort}} = -0.183$, 85% CI: -0.343 to -0.025) (Table 2) and were positively associated in mountain bluebirds (LMM, Gaussian distribution, $\beta_{\text{cort}} = 0.383$, 85% CI: 0.162 – 0.608) (Table 2). These results suggest that direct relationships between cort and fitness depend on the context of life history and species.

In contrast to provisioning, during incubation, maternal baseline cort had a positive effect on hatching success (GLMM, binomial distribution, $\beta_{\text{cort}} = 0.323$, 85% CI: 0.059 – 0.668) (Fig. 5 and Table 2) that was supported across species. The finding that lower baseline cort during incubation is linked to reduced hatching success is similar to results found in free-living house sparrows (*Passer domesticus*) (85) and tree swallows (*Tachycineta bicolor*) (86) and offers further support for the idea that down-regulation of cort can have negative reproductive effects. This suggests that lower baseline cort levels may be useful in a conservation context

as an indicator of low-quality habitat. See [Tables S8–S11](#) for a more detailed account of the effect of cort on fitness.

Conclusion

We leveraged a natural experiment in a wildlands system positioned in a large-scale spatial gradient of anthropogenic noise to uncover a consistent trend of hypocorticism and complex and, in some cases, nonlinear fitness responses to noise exposure in a community of birds. Our work provides a predictive framework for understanding how chronic noise affects wildlife that is consistent with our landscape-scale and multispecies results as well as findings from several laboratory experimental systems in vertebrates (25, 32).

Chronic noise exposure masks critical acoustic cues (8, 26, 47, 50) and can increase environmental uncertainty that alters risk perception, potentially driving reductions to provisioning rates through a trade-off between vigilance and parental care. If nestlings employ compensatory strategies to cope with demands of reduced investment, earlier fledging at smaller body size should lead to net reductions in survival and success as juveniles and adults (67–69). Surprisingly, however, we also find that medium amplitudes of noise are associated with potentially positive fitness outcomes among offspring, suggesting that the consequences of altered environmental risk perception via the introduction of sensory pollutants can be complex.

The critical discovery is that there is a strong and consistent multispecies pattern of hypocorticism in response to increased noise amplitude that is linked to negative fitness consequences. This suggests an updated framework for how noise affects wildlife and strengthens the case for reassessment of conservation physiology theoretical models. Although there is an historical bias to expect elevated basal GCs in response to exposure to chronic

Table 2. Effects of cort on fitness

Dependent variable	N	Fixed effects	Random effects	k	R ²	AIC _c	Null AIC _c	χ ²
Fitness predicted by maternal baseline cort								
Hatching success	120	Baseline cort*+ Species*	None	4	0.190	90.649	92.459	0.044
Nestling feather growth (PC1)	96	Baseline cort*– Species* Cort: species* Chicks*+ Distance*+ Tree cover*+	Pair Year	12	0.969	77.126	200.930	<0.001
Nestling body size (PC2)	96	Baseline cort+ Species* Cort: species* Distance*– Lay date*–	Site	10	0.802	99.297	184.633	<0.001
Fitness predicted by nestling baseline cort								
Nestling feather growth (PC1)	162	Baseline cort+ Species*	Site Nest ID	6	0.883	189.782	224.463	<0.001
Nestling body size (PC2)	162	Species* Lay date*–	Nest ID	6	0.720	202.290	228.856	<0.001
Fitness predicted by nestling acute-stressor induced cort								
Nestling feather growth (PC1)	161	Acute cort+ Species*	Nest ID	6	0.885	182.780	217.760	<0.001
Nestling body size (PC2)	161	Acute cort+ Species*	Nest ID	6	0.705	183.643	212.253	<0.001

Models are top models or are the highest performing models within two AIC_c that included a variable for cort. This table follows the formatting described in the legend of Table 1. Acute cort, acute stressor-induced cort; k, parameters estimated.

*Predictors that do not include zero in their 85% confidence limits; all continuous predictors are marked with the direction of their effect on the dependent variable.

stressors, a careful analysis of field and laboratory studies of diverse nonmammalian and mammalian species revealed that there is no consensus endocrine response to chronic stress (87). Our work raises a subtle but important point. There may be consistent responses, such as hypocorticism, within the context of chronic, inescapable noise exposure for avian breeding communities. However, the body of evidence suggests GC regulation is also context dependent, and rather than expecting simple generalities about GC response to hold broadly, it is more critical to document dysregulation, along with associated negative health consequences (88, 89). The next frontier in conservation physiology research may be understanding the physiological and behavioral consequences of chronic adverse experience and GC dysregulation in the context of the collective adaptive or maladaptive behavioral, immune (e.g., inflammatory), autonomic, and neuroendocrine mediator responses (i.e., those involved in growth, reproduction, and metabolism) (90, 91).

We conclude by noting that conditions at our sites are not unusually loud compared with anthropogenic noise found in many areas across the United States, or globally. In the contiguous United States, estimates of the land area exposed to even moderate amplitude increases of 10 A-weighted decibels [dB(A)] above natural levels is ~485,268.16 km² (92), and highly restricted protected areas and critical habitat for species of concern are not immune (3). A 10 dB(A) increase above natural levels translates into a 90% decrease in listening area (1, 3) (i.e., the spatial extent of detection of acoustic signals or cues)—clearly a drastically reduced perceptual world. In this era of unprecedented, large-scale human-driven environmental change, preservation or recovery of natural acoustic conditions should be a key aspect of conservation planning and is a critical step toward successful conservation of protected species.

Materials and Methods

Study System. We conducted fieldwork, following University of Colorado Boulder Institutional Animal Care and Use Committee guidelines (Protocol 1404.03), at a long-term study site in the Bureau of Land Management's Rattlesnake Canyon Habitat Management Area (RCHMA) in NW New Mexico during late spring and early summers from 2011 to 2014. The piñon (*Pinus edulis*)–juniper (*Juniperus osteosperma*) woodland and shrub grassland ecosystem of RCHMA is heavily affected by large-scale development of oil and gas infrastructure. Although developed by industry, RCHMA is remote, and animals in this region have very little contact with humans outside of minimally trafficked dirt roads and exposure to industry workers on well pads. Throughout this system, we installed a network of 240 cedar latched-roof nest boxes (53). Although nest boxes were designed to exclude common opportunistic nest predators such as Woodhouse's scrub-jay (*Aphelocoma woodhouseii*) and the least chipmunk (*Tamias minimus*) that appear largely responsible for nest predation in this system (2, 6), instances of predation by generalists such as deer mice (*Peromyscus* spp.) and bull snakes (*Pituophis catenifer sayi*) were occasionally observed at nest boxes across all noise levels.

We utilized the gradient of noise at RCHMA by placing nest boxes throughout the study area in 12 pairs of control and treatment sites, with 10 boxes per site. All sites were fully operational with nearly identical industrial equipment and similar levels of human activity on treatment and control sites (*SI Materials and Methods*). The key distinction between treatment and control sites was the presence of large compressor engines, which constantly produced high-amplitude, low-frequency noise on treatment sites (Fig. 1). Each control site was located at least 500 but no more than 1,000 m from its treatment pair, assuring that it was close enough to the treatment site to control for localized factors related to land cover composition but was far enough away to not be significantly affected by the noise from the compressor. Each control site was at least 500 m from any other noise-producing wells that were not involved in this study. Noise levels across all pairs of treatment and control sites differed significantly, while forest cover and vegetation did not (2, 53). We placed nest boxes in a circular pattern at ~75 m, 125 m, and 175 m from the center of the well pad on control sites and from the compressor on treatment sites (Fig. 1). By placing the boxes at uniform distances from site centers we control for the effect of disturbance created by industry workers servicing equipment.

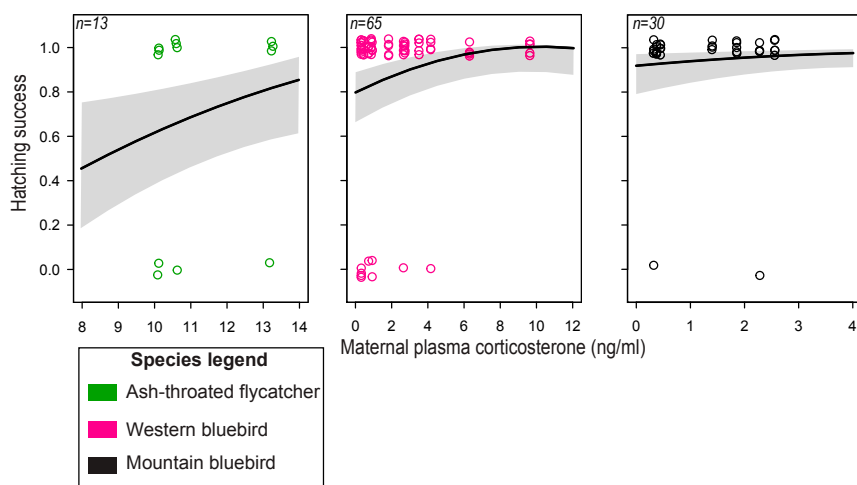


Fig. 5. Adult female baseline cort, measured during incubation, was positively associated with hatching success. The gray-shaded areas indicate the 85% confidence intervals for each estimated effect.

Nest Monitoring. We began monitoring nest boxes in early May each year, coinciding with the start of breeding season. Following a system-wide check for nesting activity, each box was monitored biweekly. Upon recording nesting activity in a box, we rated each nest as 25, 50, 75, or 100% complete to prioritize further monitoring efforts. We checked complete nests every other day until at least one egg had been laid. However, logistical constraints sometimes restricted searching efforts. When more than one egg was found in a nest, we followed standard methodology (93, 94) and used natural history information on egg-laying intervals and incubation periods (57, 95, 96) to back-calculate the initial lay date. Observations continued until the date when the first chick of each brood hatched, or “day zero.” These data were used to schedule the nestling sampling date, which allowed the chicks to develop without unnecessary disturbance by our research team until day 12.

Capture Methods and Hormone Assays. Nestlings were in pre fledging stage during sampling and were hand-captured from the box. We were not able to differentiate between nestling sexes. Adults were hand-captured with the use of a sliding-door trap on the nest box initiated by a researcher hidden behind a bush and holding a line attached to the hole-block. We focused our adult study on breeding females only, and we identified females through behavior and coloration and, after capture, using the presence or absence of a brood patch. Thus, we were able to take into full account the effects of parental sex and life stage, which, when not controlled, can obscure important signals due to innate differences in GC levels between these groups (97). Once the target adult female entered the box, the line was pulled, and the timer was started.

Blood was taken within 3 min after capture from each individual to measure baseline levels of stress hormone (98). Less than 100 μ L of blood per individual was collected into heparinized hematocrit tubes from a puncture by a sterile needle in the brachial vein and was stored on ice until centrifugation. Birds were banded with standard issue metal bands from the US Geological Survey Bird Banding Laboratory (#22837). We also measured body mass, wing length, tail length, and tarsus length for a general gauge of overall condition after baseline samples had been collected. After 10 min of restraint in a cloth sack, we sampled individuals for acute stressor-induced cort levels. We recognize that our protocol is shorter than typical stressor-restraint protocols, and we present these data as indicators of HPA responsiveness and not the maximum amount of cort released in response to a stressor. However, 10 min of restraint is likely enough time to elicit maximum cort release in birds (99–101). Due to concerns about nest abandonment, which reduced sampling feasibility in these species, we do not include acute stressor-induced cort measurements from adults. Details on sample handling, accuracy, and variation, especially with regard to low concentrations of cort, are available in *SI Materials and Methods*.

Measurement of Noise and Other Habitat Factors. We measured the equivalent continuous sound level [L_{eq} , dB(F), fast response, re. 20 μ Pa] for 1 min at every nest box using a Larson–Davis System 824 sound pressure meter. See Kleist et al. (53) and *Fig. S1* and *SI Materials and Methods* for more details on sound measurements. Tree cover was measured using ArcGIS and National Land Cover Dataset following methods described by Kleist et al. (53). We include tree cover because all three focal species prefer open, sparse shrublands rather than closed, forested habitats (57, 95, 96). Additionally, we include the dis-

tance to the center of the well pad to control for the effect of nest box’s proximity to the well pad, which, irrespective of noise, may include low levels of chemical pollution and the infrequent presence of humans.

Temporal and Life History Factors. Baseline and acute stressor-induced levels of cort can relate to seasonality, life stages, and brood size, and we gathered data to control for these effects (21). We included sampling time as a fixed effect because GC levels are known to fluctuate throughout the day (25, 102). We included lay date in models since this variable corresponds with peaks in food availability and likely affects cort, relative to individual arrival times. Recent work suggests that cort levels are context dependent (27, 66, 103) and that, within the breeding attempt, brooding and provisioning might require different amounts of cort; i.e., increased cort can facilitate provisioning (104). To control for these differences, we differentiate between blood drawn from brooding or provisioning adult females. Additionally, nest investment and reproductive potential can influence cort levels (103), and although we are not able to test directly for an effect of maternal age on nestling response, we do include a nest ID variable to control for individual effects. Finally, the brood size in each nest was recorded to control for the increased challenge of rearing large broods, which has been shown to affect incubation and lead to decreases in nest success (105).

Accounting for Potential Self-Sorting. In the event that lower-quality birds are relegated to or inadvertently select habitats with more noise exposure, the results of an analysis seeking to determine the effect of noise per se would potentially be biased. We tested whether this was a possibility by measuring body mass of all adult females, which is a reliable indicator of condition (106), before performing further analyses. We created linear models with noise and female body weight to determine if any correlation existed between noise levels at the nest box [dB(F)] and female condition. Across RCHMA, we found no evidence that heavier, higher-quality adult females were preferentially selecting quieter locations for nesting (*Table S1*), and therefore any variation in fitness and stress hormones is likely a result of habitat factors present at the nest site.

Model Testing Framework. We used LMM and GLMM models with the lme4 package in the R statistical language, including a fixed term for “species,” to test for effects of noise on cort and several measures of fitness, including hatching success and nestling body condition. We also tested for any relationship between cort and fitness (27). When species was significant as a fixed effect, we examined species-specific models.

The first model set examined the effects of noise on both nestling and adult female cort levels and included continuous fixed effects for noise, species, tree cover, distance to well pad, lay date, time of day, brood size and, in adults, a categorical effect for life stage, included as either incubation or provisioning. We tested baseline cort in adults and both baseline and acute stressor-induced cort, measured 10 min after capture, in nestlings.

The second model, which is the first of two models focused on uncovering the effect of noise on fitness, explored the relationship between noise and egg-hatching success. We defined hatching success as a binomial response in which each egg that was laid in a nest was included; those that hatched were marked as a 1, and those that did not hatch were marked as 0 (107). The

binomial response term for hatching was included in models with noise, species, lay date, distance to well pad, tree cover, and clutch size.

In addition to measuring the effect of noise and other factors on hatching success, a direct measure of reproductive success, we created a third modeling set that included nestling condition as a response term. Nestling developmental changes can be a subtler but equally important indicator of fitness (52, 77). We used principal components analysis (PCA) with varimax rotation (principal function in the psych library for R) to load measurements of nestling wing chord (in millimeters), rectrices (in millimeters), tarsus length (in millimeters), and mass (in grams) onto appropriate axes. These measurements were all taken on the 12th day after hatching, because that is the final day where nest visitation is unlikely to instigate disturbance-induced pre fledging (North American Bluebird Society, www.nabluebirdsociety.org). These morphological measures loaded on two axes with PC1 explaining 47% and PC2 37% of the variation in the data (Table S2). Wing chord length and length of rectrices loaded strongly onto PC1, while mass and tarsus length loaded strongly onto PC2; because of these loadings, we named these axes "PC_{feather}" and "PC_{size}," respectively. We placed these axes as response terms in models that include fixed effects for noise, species, tree cover, distance to well pad, lay date, and brood size. Because nestling mass is known to fluctuate throughout the day, we also included a term for time of day in model selection for PC_{size}. After initial exploration of data distributions, we included both PC_{feather} and PC_{size} as second-order polynomials, suggesting that developmental effects of noise might vary nonlinearly with amplitude. In experimental research with humans, vigilance is known to peak at medium amplitudes of noise (108). This has important implications, via noise-mediated foraging-vigilance trade-offs (7), and could translate to reduced provisioning rates and altered development in nestlings, in a similar nonlinear fashion.

Finally, we explored the relationship between cort and fitness. In three separate models, we incorporated nestling body condition as a response to nestling baseline cort, nestling acute stressor-induced cort, and maternal baseline cort measured during provisioning. We also analyzed the effect of maternal baseline cort measured during incubation on hatching success. For all cort-fitness models we included an interaction between cort and species, as cort levels are known to vary systematically across species. Although the focus of this paper is to explore the effect of acoustic habitat disturbance on

physiology and fitness, and not the effect of maternal cort on nestling growth, we included these models to more fully examine if changes to baseline cort resulting from noise exposure are linked to negative fitness consequences. We did not use noise as a predictor in these models to better isolate effects of maternal cort on fitness-relevant measures.

For all models, we included random effects terms to control for variation in data attributable to environmental factors associated with pair, site, and nest box (Fig. 1) and also included a random effect for year. Nestling cort and fitness models included a random effect for Nest ID to control for brood identity in nestlings and for multiple breeding attempts in adults.

Model selection was conducted using an information criterion approach to compare AIC_c scores between models. All continuous fixed effects were transformed to z-scores using the scale function in R, which allows direct comparison of effects and improves model fit. After initially fitting the full model, random effects that explained near-zero variance (variance ≤ 0.0001) were removed to improve the fit of the model (109). Additionally, we refit models as GLMM if all random effects were removed during model selection. We considered models with all combinations of hypothesized predictor variables and designated all models within two ΔAIC_c and that differed from the null model with identical random effects as determined by a likelihood ratio test as strongly supported. We calculated effect sizes and 85% CIs for individual predictors from supported models (7, 110). For full results, including effects of other predictors and model selection, see Tables S3–S7. All data and the R code used to produce this work will be made available online in a Dryad digital data repository.

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