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Contaminant-by-environment interactive effects on animal behavior in the context of global change: Evidence from avian behavioral ecotoxicology

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Abstract: The potential for chemical contaminant exposure to interact with other stressors to affect animal behavioral responses to environmental variability is of mounting concern in the context of anthropogenic environmental change. We systematically reviewed the avian literature to evaluate evidence for contaminant-by-environment interactive effects on animal behavior, as birds are prominent models in behavioral ecotoxicology and global change research. We found that only 17 of 156 (10.9%) avian behavioral ecotoxicological studies have explored contaminant-by-environment interactions. However, 13 (76.5%) have found evidence for interactive effects, suggesting that contaminant-by-environment interactive effects on behavior are understudied but important. We draw on our review to develop a conceptual framework to understand such interactive effects from a behavioral reaction norm perspective. Our framework highlights four patterns in reaction norm shapes that can underlie contaminant-by-environment interactive effects on behavior, termed exacerbation, inhibition, mitigation and convergence. First, contamination can render individuals unable to maintain critical behaviors across gradients in additional stressors, exacerbating behavioral change (reaction norms steeper) and generating synergy. Second, contamination can inhibit behavioral adjustment to other stressors, antagonizing behavioral plasticity (reaction norms shallower). Third, a second stressor can mitigate (antagonize) toxicological effects of contamination, causing steeper reaction norms in highly contaminated individuals, with improvement of performance upon exposure to additional stress. Fourth, contamination can limit

behavioral plasticity in response to permissive conditions, such that performance of more and less contaminated individuals converges under more stressful conditions. Diverse mechanisms might underlie such shape differences in reaction norms, including combined effects of contaminants and other stressors on endocrinology, energy balance, sensory systems, and physiological and cognitive limits. To encourage more research, we outline how the types of contaminant-by-environment interactive effects proposed in our framework might operate across multiple behavioral domains. We conclude by leveraging our review and framework to suggest priorities for future research.

Keywords: behavioral ecotoxicology, multiple stressors, chemical contaminants, interactive effects, behavioral plasticity, behavioral reaction norms

1. Introduction: Climate change, urbanization, deforestation, and chemical pollution are among the multifaceted drivers of anthropogenic environmental change that are reshaping ecosystems at unprecedented rates, and exposing organisms to multiple abiotic and biotic stressors (IPCC 2021; Early et al. 2015; Burgess et al. 2018). A question of pressing research and conservation interest is whether organisms will cope with these stressors, and adjust to rates of environmental change that threaten to exceed those of microevolution. Due to their plasticity, changes in behavioral patterns constitute primary defences against rapid environmental change (Sih 2013; Wong and Candolin 2015). For instance, foraging plasticity can allow animals to adjust to climate change-related shifts in resource distribution (Grémillet et al. 2012; Gilmour et al. 2018), and plasticity in acoustical signals facilitates maintenance of communication systems in environments impacted by anthropogenic noise pollution (Bermúdez-Cuamatzin et al. 2011).

Chemical contaminant exposure is a potent factor that threatens to impair animal behavioral responses and resiliency under global change scenarios. Endocrine-disrupting, energetic and neurotoxic effects of contaminants, including metals, pharmaceuticals, persistent organic pollutants (POPs) and diverse pesticides, can alter animal behavior across diverse domains by affecting physiological and neurological control mechanisms and limiting the capacity for behavioral plasticity (Blévin et al. 2017; Saaristo et al.

2018; Bertram et al. 2022). Organisms are exposed to diverse contaminants due to long-term persistence of banned chemicals in ecosystems (POPs), continued use of chemicals deemed less toxic or essential, and continual development of new chemicals, many of which are of emerging concern (González-Rubio et al. 2021). Contaminant exposure is widespread, with long-range transport mechanisms and bioaccumulation causing some contaminants (e.g. POPs, mercury (Hg)) to exceed toxicological thresholds even in remote areas, such as polar regions (AMAP 2016, 2021). Furthermore, anthropogenic environmental change threatens to increase contaminant bioavailability and toxicity, exacerbating effects on animal physiology and behavior (Hooper et al. 2013; McKinney et al. 2015). For example, melting of the cryosphere due to climate change is releasing legacy POPs into the environment in polar regions (Noyes et al. 2009, AMAP 2016), and conversion of inorganic Hg to toxic methylmercury is accelerated in warming oceans (MeHg) (Cossa 2013).

As recognized by a growing number of researchers, forming ecologically realistic predictions regarding contaminant effects on animal behavior and fitness under global change scenarios will require adopting a multiple stressor perspective (Goutte et al. 2018; Esparza et al. 2022; Smith et al. 2022). Indeed, in addition to influencing environmental contaminant levels, anthropogenic environmental change is reconfiguring resource distributions, thermal conditions, and predation pressure, among other stressors, challenging animal behavioral capacity and reproductive performance (Wong and Candolin 2015). For example, Arctic animals including some seabird and marine mammal populations are facing major declines in sea ice-associated resources concurrent with rising Hg contamination, leading to behavioral and energetic challenges (Morris et al. 2022; Tartu et al. 2022). Ramifications of contaminant exposure for animal behavioral patterns might be magnified given concurrent exposure to other stressors associated with environmental change, generating synergistic (more than additive) or emergent (novel synergistic) effects which threaten to destabilize populations (Bustnes et al. 2005; Goutte et al. 2018). On the other hand, antagonistic (less than additive) interactive effects of multiple stressor exposure on biological traits are also quite commonly documented (Crain et al. 2008; Wilson et al. 2021). We lack knowledge of the

prevalence of contaminant-by-environment interactive effects on animal behavior, making it difficult to evaluate implications in the context of anthropogenic environmental change.

To address this deficit, we evaluated the evidence for contaminant-by-environment interactive effects on animal behavior by systematically reviewing the avian behavioral ecotoxicological literature. Birds provide an excellent model system for this work, as they are prevalent study species in behavioral ecotoxicology, and often occupy high trophic positions, deeming them susceptible to bioaccumulation and toxicological effects (Burger and Gochfeld 2005; Espín et al. 2016; Mills et al. 2020). For the purpose of our review, we broadly defined a stressor as any factor that reduces environmental favorability, generally by moving the environment away from conditions to which organisms are optimally adapted. For example, stressors considered by studies identified in our review included resource shortage, parasitism, predation risk, and variability in climatic conditions. We report on the number of avian behavioral ecotoxicological studies that have considered contaminant-by-environmental stressor interactive effects, and the number of these that have found evidence for interactions. We also describe the findings of studies that have found evidence for interactions, which stressors, contaminants and behavioral domains were involved, and whether synergistic or antagonistic effects on behavioral changes were entailed.

Moreover, we leveraged results from our review to develop a general conceptual framework to understand contaminant-by-environment interactive effects on animal behavior from a behavioral reaction norm perspective. Behavioral reaction norms describe individual-specific behavioral responses to changes in environmental conditions (Dingemanse et al. 2010). The premise underlying our framework is that exposure to contaminants alters behavioral reaction norms of individuals with respect to gradients in other environmental stressors, and vice versa (i.e. individuals in poor body condition due to resource shortage may respond differently to contamination), generating interactive effects on behavior. Our aim in presenting this framework is not to elucidate all possible mechanisms (e.g. physiological pathways, modes of toxicity) underlying specific contaminant-by-environment interactive effects on animal behavior, or suggest all forms that such interactions might take. Rather, our aim is to illustrate how

adopting a behavioral reaction norm perspective can lead to new insights into synergistic and antagonistic contaminant-by-environment interactive effects on behavior, by leading to more in-depth consideration of the different ways in which individuals may alter, or fail to alter, behavior across multi-dimensional stress gradients. To encourage more research, we used our conceptual framework in combination with our literature review to propose how contaminant-by-environment interactive effects, driven by nonparallel behavioral reaction norms, might operate across diverse avian behavioral domains. We conclude by highlighting priorities for future research within the contexts of multiple stressor research and global change biology, and guided by a behavioral reaction norm approach.

2. Systematic review: We used ISI Web of Science to systematically review the avian behavioral ecotoxicological literature and assess the evidence for contaminant-by-environment interactions. Specifically, we combined three topic searches (covering the title, abstract, author keywords, and keywords plus), one involving behavior, one contaminants, and one birds. Keywords for the behavior search were: *behav** OR *movement* OR *parent** OR *provisioning* OR *personality* OR *aggress** OR *boldness* OR *risk-taking* OR *neophob** OR *forag** OR *feed** “*egg laying*” OR *GPS* OR *accelerometer* OR *incubat** OR *migrat** OR *social* OR *mating* OR *nest def** OR *flying* OR *flight* OR “*sexual display*” OR *sing** OR *courtship* OR *mating* OR “*mate choice*” OR *cognit** OR *problem-solving* OR *innovation* OR *predation* OR *predatory* OR *antipredator** OR *swim** OR *dive* OR *diving* OR “*predator recognition*” OR *escap**. Keywords for the contaminants search were: *contamin** OR *pollut** OR “*persistent organic pollut**” OR *metal** OR *Hg* OR *Cd* OR *Pb* OR *arsenic* OR “*endocrine disrupt**” OR “*flame retard**” OR *pesticide** OR *herbicide** OR *insecticide** OR *fungicide** OR *aldrin* OR *chlordane** OR *dichlorodiphenyltrichloroethane* OR *DDT* OR *dieldrin* OR *endrin* OR *heptachlor* OR *hexachlorobenzene* OR *mirex* OR *toxaphene* OR “*polychlorinated biphenyls*” OR “*polychlorinated dibenzo-p-dioxin**” OR “*polychlorinated dibenzofuran**” OR “*polybrominated diphenyl ether**” OR *hexabromocyclododecane* OR “*perfluorooctane sulfonic acid**” OR “*perfluorooctanoic acid*” OR “*short-chain chlorinated paraffins*” OR *pentachlorophenol* OR *hexachlorocyclohexane** OR *endosulfan* OR “*polychlorinated naphthalenes*”

OR “perfluorocarboxylic acids” OR “perfluorosulfonic acid*” OR “perfluorohexane sulfonic acid” OR “perfluoroalkyl acid*” OR “organophosphate ester*” OR dacthal OR chlorpyrifos OR trifluralin OR pentachloronitrobenzene OR “polycyclic aromatic hydrocarbon*” OR pentachloroanisole OR microplastic* OR bromoanisole OR “hydroxylated PBDE*” OR “methoxylated PBDE* . Keywords for the bird search were: bird* OR avian OR passerine OR raptor OR seabird OR waterbird OR eagle OR vulture OR condor. With these search terms we aimed to cover a diverse array of contaminants, behavioral domains and bird species. However, as a caveat, we could not explicitly target all contaminants, behavioral types and species in this search. We included field and laboratory studies on non-domesticated birds, and correlational and experimental work. We did not include studies regarding how behavior affects contamination (e.g. trophic foraging position affects contamination; Sebastiano et al. 2017), but acknowledge the bidirectionality of contamination-behavior relationships (Sih et al. 2015). We conducted the final search on 12 February, 2023.

Our search returned 5,826 results, including studies published between 1975 and early 2023. We screened abstracts to identify 190 studies of potential relevance. After reading full texts, 132 studies were retained. We identified an additional 24 studies by reviewing literature that cited, or was cited by, papers that met our criteria, for a total of 156 studies considering relationships between contaminant exposure and behavioral traits (see Table S1 for a full listing of these studies, including behavioral traits, contaminants considered, and effects identified). We thoroughly read these 156 studies to determine whether contaminant-by-environment interactions were considered and statistically significant ($\alpha = 0.05$), and the nature of both non-interactive and interactive effects. The results of our systematic review are summarized in Figure 1 and Table S1.

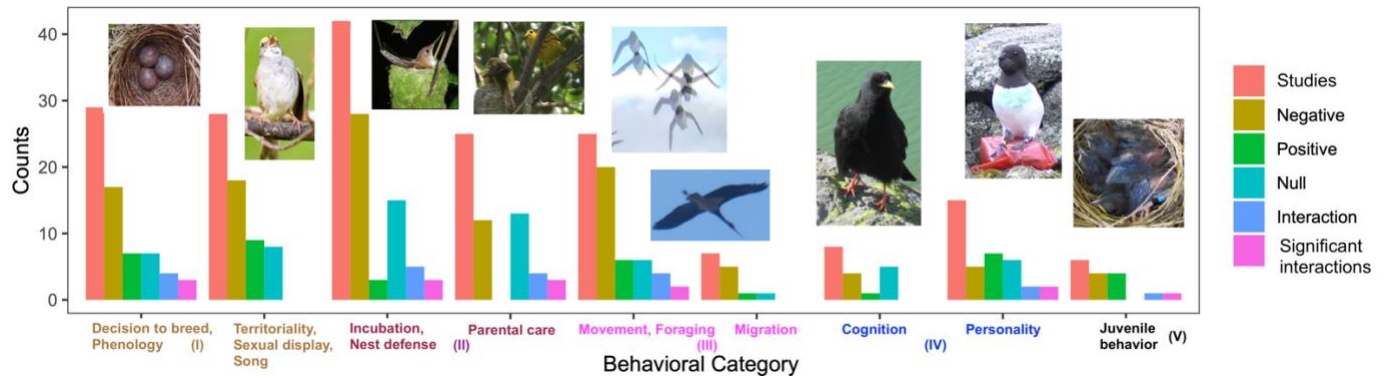


Figure 1. Avian behavioral ecotoxicological studies identified in a systematic review, including the number of studies that considered different behavioral types (out of 156), which types of effects were observed ($\alpha = 0.05$), how many studies considered contaminant-by-environment interactions, and how many found significant interactive effects. We provide predictions regarding potential contaminant-by-environment interactions for main behavioral domains I-IV, which are separated by color. Some studies are categorized into multiple domains, including 5 studies that considered interactions, such that totals exceed 156. Photo credits: Andrea Grunst, Melissa Grunst, and Indiana State University Photo Services (singing sparrow).

3. Evidence for contaminant-by-environment interactions

3.1. Prevalence and results of studies investigating interactions: Only 17 of the 156 (10.9%) avian behavioral ecotoxicological studies that we identified in our review explored contaminant-by-environment interactions. In Table 1, we detail the results of these studies, which types of interactive effects they involved (synergy, antagonism, etc.), and how they can be classified within our behavioral reaction norm-based framework, which is described below. These studies involved multiple behavioral domains, including parental (9 studies) and foraging (3 studies) behaviors in free-living birds, and parental behavior (1 study), movement and foraging (3 studies), risk-taking (1 study), and righting responses (personality) (1 study) investigated in the laboratory. In addition, a diverse array of chemical contaminants (metals, POPs) and additional stressors (parasitism, resource shortage, weather conditions) were considered (Table 1). Thirteen of the 17 studies (76.5%) found at least some evidence for interactions, suggesting that contaminant-by-environment interactive effects on behavior are understudied but likely to be important.

The majority of the studies (10/13) that found interactive effects suggested that behavioral correlates (or effects) of contamination were aggravated (synergy), or only manifest (emergent effect), when

individuals were exposed to additional stressors, suggesting that behavioral toxicological effects of contamination became more severe upon multiple stressor exposure. These 10 studies involved a spectrum of different behavioral domains, and interactions with diverse environmental stressors (Table 1). For example, parental performance of glaucous gulls (*Larus hyperboreus*) contaminated with organochlorines (OCs) varied with ecological conditions that modified flight costs during foraging. Specifically, chick growth rate was reduced for OC-exposed females in an area where feeding on fish predominated and flight costs were high, suggesting insufficient parental provisioning. In contrast, chick growth rate was not reduced for contaminated females in areas where feeding on bird eggs predominated, and flight costs were low (Bustnes et al. 2005). Thus, females highly contaminated with OCs appeared unable to maintain parental provisioning performance when faced with high flight costs, generating a synergistic (more than additive) effect of OC-contamination and challenging foraging conditions on parental performance. Similarly, in great skuas (*Stercorarius skua*), females highly contaminated with OCs insufficiently provisioned chicks (as evaluated through chick growth rates) when not provided with supplemental food, but not when food was supplemented and thus readily available (Bustnes et al. 2015). Also in the context of foraging, in a recent study on little auks (*Alle alle*), birds highly contaminated with Hg took longer inter-dive breaks than less contaminated individuals, but only when making long duration dives. As dive duration increased with sea surface temperature, reflecting changes in the distribution of copepod prey, these results suggest that effects of Hg on dive bout patterning could be accentuated in warming oceans. However, note that increasing the lengths of inter-dive breaks allowed little auks highly contaminated with Hg to maintain dive duration, illustrating that behavioral plasticity in one trait can buffer individuals against changes in other essential behaviors or fitness traits (Grunst et al. 2023).

Other environmental stressors that have been implicated in accentuating the behavioral effects of chemical contamination include predation pressure and high temperatures. Mercury-exposed zebra finches (*Taeniopygia guttata*) exhibited greater foraging latency under high, but not low, predation risk (Kobiela et al. 2015). Therefore, difference in boldness and foraging strategy only became manifest given elevated predation risk, perhaps due to neurotoxicological effects of Hg on risk perception, or lesser

escape capacity in Hg-contaminated birds. In the context of temperature variation, juvenile killdeer (*Charadrius vociferous*) exposed to PBCs in ova displayed faster righting responses relative to controls only when incubated at suboptimally high temperature (39°C). Faster righting responses were interpreted as reflecting hyperactivity and anxiety (Lunny et al. 2020). Therefore, PBC-induced changes in the development of behavioral traits only emerged under elevated temperatures, perhaps due to increased contaminant (PCB) toxicity at high temperature.

In contrast, only a few (3/13) studies suggested that behavioral correlates (or effects) of contamination were reduced (antagonized, less than additive) in association with exposure to a second stressor. In these few cases, antagonistic effects appeared to arise via different pathways. Firstly, in common eiders (*Somateria mollissima*), birds given an anti-parasite treatment exhibited a stronger negative effect of lead (Pb) exposure on survivorship than controls, suggesting that parasites reduce toxicological effects of lead. However, no interactive effect of parasitism and Pb on reproductive behavior was found, and whether effects on survivorship were mediated through behavior is unclear. Parasites might sequester contaminants, mitigating toxicological effects, and causing increases in the behavioral or physiological performance of individuals highly exposed to contaminants relative to less exposed counterparts (Morrill et al. 2019). On the other hand, because this study utilized an anti-parasitism treatment, the possibility that the anti-parasitism drug acted synergistically with lead exposure to elevate stress levels in contaminated birds cannot be excluded.

In a second study suggesting an antagonistic contamination-by-environment interactive effect, female common eiders with elevated egg Hg concentrations displayed lesser increases in incubation interruptions and lay dates (lesser changes in behavior) with warm temperature, and conversely lesser decreases in interruptions with cold temperature, as compared to less contaminated counterparts (Smith et al. 2022). Thus, Hg contaminated females displayed lower levels of behavioral plasticity in incubation patterns with respect to temperature as compared to less contaminated females, which could limit adjustment of incubation rhythms to environmental conditions. However, whether responses to temperature observed in less contaminated females were in fact adaptive is unclear, as fitness correlates were not available.

Furthermore, as Hg levels were measured only in eggs, the contamination status of females was not certain. Verification of the contamination status of females, and a functional understanding of the physiological, energetic and toxicological drivers of variation in incubation patterns would thus be needed to better understand the results of this study.

Finally, in a third study involving an antagonistic effect, Hg-exposed great egrets (*Ardea albus*), took longer to capture prey as compared to controls given high prey detectability, but not when prey detectability was reduced (Bouton et al. 1999). This finding is contrary to the intuitive prediction that challenging foraging conditions might exacerbate effects of contamination on foraging performance, leading to a synergistic effect. However, the observed results likely arise through dampening of a positive functional response to increasing prey detectability in contaminated birds, for instance, if contaminated birds are less motivated to capture detected prey. This example illustrates that more challenging foraging conditions might not always cause the foraging performance of more and less contaminated (or otherwise stressed) individuals to diverge. Rather, contamination could render individuals less motivated or able to capitalize on favorable foraging conditions.

3.2. Investigation of functional mechanisms by studies involving interactions: In addition to identifying a dearth of avian behavioral ecotoxicological studies that have investigated contaminant-by-environment interactive effects, our review highlighted a scarcity of studies that pursued a functional understanding of mechanisms underlying such interactions. Specifically, only 2 (11.7%) of the 17 studies that investigated contaminant-by-environment interactions also explored physiological mechanisms underlying toxicological effects. These studies both explored endocrinology in seabirds as a potential mechanism, and both found inconclusive support for interactive effects. In one study, Arctic-breeding thick-billed murre (*Uria lomvia*) highly exposed to Hg were found to display altered triiodothyronine (T3) levels only in years with abnormally advanced sea ice retreat, when foraging conditions were likely poor. Increased T3 was in turn associated with reduced time engaged in energetically-intensive diving behavior. Thus, the authors suggested that Hg-associated metabolic dysregulation caused by disruption of

the hypothalamus-pituitary-thyroidal (HPT) axis might force changes in energetically expensive foraging patterns only given elevated energetic stress, generating emergent behavioral effects (Esparza et al. 2022). However, the relationship between Hg and T3 levels was opposite in the two years with advanced sea ice breakup, complicating interpretation of results. In the second study, black-legged kittiwakes (*Rissa tridactyla*) were implanted with corticosterone (CORT), the major avian stress hormone, to assess the hypothesis that elevation of CORT under stressful environmental conditions (e.g. resource shortage) might be implicated in aggravating effects of Hg on reproductive performance (Tartu et al. 2016). CORT exerts effects on energetics that could alter toxicological effects of Hg exposure, notably including increasing glucose metabolism and directing energy expenditure away from reproduction by down-regulating the hypothalamus-pituitary-gonadal (HPG) axis (Wingfield et al. 1998). However, no interactive effect between Hg levels and CORT implantation were found. Other studies have investigated toxicological effects of contaminants on physiology, neurology and sensory systems, without considering interactive effects with other environmental stressors, suggesting potential functional pathways through which interactions could operate (Table S1). However, more studies that investigate the physiological and toxicological mechanisms underlying contaminant-by-environment interactive effects are needed to enhance our understanding of these interactions and increase predictive power.

Table 1. Studies involving interactive effects of contaminant exposure and environmental variables on behavior in non-domesticated birds. We list authors, study species, behavioral category (Reproductive I = pre-incubation reproductive behaviors, Reproductive II = incubation and parental care), and contaminant type and concentration, the additional environmental stressor considered, results including coefficient estimates when reported, classification based on standard multi-stress terminology (synergy, antagonism, etc.), and classification within our behavioral reaction norm-based conceptual framework.

| | AUTHORS | SPECIES | TYPE BEHAVIOR | CONTAMINANT TYPE/CONCENTRATION | ENVIRONMENTAL STRESSOR | RESULTS | CLASSIFICATION, MULTI-STRESS | CLASSIFICATION, BEHAVIORAL REACTION NORM FRAMEWORK |
|---|-------------------------|---|------------------------|--|---|--|---------------------------------|---|
| 1 | Keith and Mitchell 1993 | Ringed turtle dove (<i>Streptopelia risorii</i>) | Reproductive II and II | POPs: DDE | Resource availability, Food restriction of 10% | Food restriction of 10% reduced reproductive success by 50% in controls, and 87% in DDE treated birds due to altered reproductive behavior. Reduction in reproductive success for DDE bird with ad- libitum food was 23%. | Synergy | Exacerbation |
| 2 | Bouton et al. 1999 | Great egret (<i>Ardea albus</i>) | Movement, Foraging | Metal: Hg, 0.5 or 5 mg MeHg chloride per kilogram of food | Difficulty of foraging conditions, as determined by prey detectability | Hunting in a pool where prey were more camouflaged reduced prey capture rate. Blood and down Hg, and Hg exposure treatment group, were related to increased time to capture prey when prey detectability was high, but not low. This suggests that control birds experienced greater magnitude decreases in | Antagonism | Convergence |

| | | | | | | | | |
|---|-----------------------------------|--|--------------------|---|---|---|----------------------|----------------|
| | | | | | | prey capture due to poor prey detectability than did Hg exposed birds. | | |
| 3 | Nocera and Burgess 2002 | Common loon (<i>Gavia immer</i>) | Movement, Foraging | Metal: Hg tHg, Mean \pm SE (range) = 4.34 \pm 2.1 (0.8-11.18) μ g/g ww blood | Prey abundance (fish biomass): Mean \pm SE (range)= 450 \pm 210 (1.1-1426) g/10 traps per day | No evidence for plasticity in dive behavior as prey abundance changed among lakes or seasonally. No effect of Hg on behavior or behavioral plasticity. | Additive | No interaction |
| 4 | Bustnes et al. 2005* | Glaucous gulls (<i>Larus hyperboreus</i>) | Reproductive II | POPs: OCs Range in means per year: HCB: 12.5-20 PCBs: 326-431 DDE: 58-98 ng/g ww blood | Difficulty of foraging conditions and energetic costs based on foraging on fish versus bird eggs | Chick growth rates reduced for contaminated females feeding on fish, for which flight costs were high, suggesting insufficient parental provisioning. Chick growth not reduced for contaminated females feeding on bird eggs, for which flight costs were low. Beta Coefficients in fish- feeding group: PCBs: -0.075, HCBs: - 0.110, DDE: -0.099 Oxychlordan: -0.074. | Synergy/ Emergent | Exacerbation |
| 5 | Bustnes et al. 2006 ^{8a} | Glaucous gulls (<i>Larus hyperboreus</i>) | Reproductive II | POPs: OCs Means \pm SE: HBC: 14.6 \pm 2.1, Oxychlordan: | Parasitism | Anti-parasite treatment during the incubation stage removed a negative effect of OCs on male | Synergy/ Emergent | Exacerbation |

| | | | | | | | | |
|---|--------------------------|--|-----------------------|---|---|--|----------------------|----------------|
| | | | | 11.8 ± 1.8, DDE: 74.6 ± 9.6, PCB: 373.6 ± 59.2 ng/g ww blood | | nest success, presumably by enhancing male reproductive behavior. No effect found in females. In a log-odds model, coefficients were: OC = -2.83, Anti-parasite = -6.73, Interaction = 4.83. The interaction effect predominates, leading to a pattern of synergy. | | |
| 6 | Adams and Frederick 2008 | White ibis (<i>Eudocimus albus</i>) | Movement, Foraging | Metal: Hg 0, 0.05, 0.1, 0.3 mg MeHg/kg/day | Foraging habitat complexity (abundance of vegetation and prey refugia) | Foraging efficiency reduced by habitat complexity, and non-linearly related to MeHg exposure, with control and high exposure groups showing lower foraging efficiency. MeHg and habitat complexity did not interact to affect foraging efficiency. | Additive | No interaction |
| 7 | Bustnes et al. 2015* | Great skua (<i>Stercorarius skua</i>) | Reproductive II | POPs: PBDEs, and OCs, Mean ± SE: ΣBDE = 8.6 ± 1.1 ΣOC = 621.7 ± 83.3 (values for females in Iceland colony, where interactive effect was found) | Resource availability, as determined by supplemental feeding | Female POP concentrations negatively correlated with growth rates of first chicks in control, but not food supplemented nests, suggesting insufficient provisioning of chicks by highly contaminated | Synergy/ Emergent | Exacerbation |

| | | | | | | | | |
|---|------------------------|---|------------------------------------|--|----------------|--|----------------------|----------------|
| | | | | | | females only under resource limitation. Estimates were given for effects in the control rather than experimental group. The strong negative interactive effect within the more stressed control group leads to synergy/exacerbation. | | |
| 8 | Kobiela et al. 2015 | Zebra finch (<i>Taeniopygia guttata</i>) | Movement, Foraging, Personality | Metal: Hg 1.2 mg/g MeHg in food, from embryonic stage (parents exposed) into adulthood. Blood Hg (mean ± SE (range)): Controls: 0.07 ± 0.09 (0.01-0.33) Dosed: 13.93 ± 3.60 (7.96-24.79) µg/g ww | Predation risk | Mercury exposed birds took 18 min longer to forage under high predation risk, but not given low risk. | Synergy/ Emergent | Exacerbation |
| 9 | Provencher et al. 2017 | Common eider (<i>Somateria mollissima</i>) | Reproductive I | Metal: Hg, In two study years, Blood Hg (mean ± SE) averaged: 0.43 ± 0.06 and 0.47 ± 0.06 µg/g ww. | Parasitism | Anti-parasite treatment increased probability of nesting among late arrivals and birds in poor condition, but Hg levels had no effect independently or in interaction with anti-parasite treatment. Low Hg burdens could | Additive | No Interaction |

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|----|---------------------|--|-----------------------|---|--|---|---|---|
| | | | | | | explain the lack of effect of Hg. | | |
| 10 | Tartu et al. 2016 | Black-legged kittiwakes (<i>Rissa tridactyla</i>) | Reproductive II | Metal: Hg Blood Hg (range): Males: ~0.65-1.75 µg/g dw Females: ~0.5-1.25 µg/g dw | Manipulated CORT levels (CORT is predicted to be elevated under challenging environmental conditions (e.g. resource shortage)). | Hg levels negatively related to number of chicks reared in males, suggesting impaired provisioning behavior. Hatching rates not related to Hg, suggesting no effects on incubation. CORT implants reduced hatching success, but did not affect relationships between Hg, prolactin and reproductive outcomes. | Additive | No interaction |
| 11 | Goutte et al. 2018 | South polar skua (<i>Catharacta maccormicki</i>) | Reproductive I and II | POPs: PCBs, OCPs (DDT, CHL), HCB, Mirex: ~44.7-897.8 ng/g lw DDT: ~148.4-2697.3 ng/g lipid wt. | Overall environmental stress levels, as assessed by CORT levels. | Skuas with high mirex and DDT levels defended nests less only in a year when CORT levels were high. Thus, high CORT, which is suggestive of environmental challenge (e.g. resource shortage) were associated with emergence of the contamination effect. | Synergy/ Emergent | Exacerbation |
| 12 | Morrill et al. 2019 | Common eider (<i>Somateria mollissima</i>) | Reproductive I | Metal: Pb Geometric mean (range): 0.0078 (0.0073–0.0084) mg/kg ww | Parasitism | Negative relationship between Pb levels and survivorship observed only in anti-parasitism treated group, suggesting | Antagony (survivorship) Additive (reproductive behavior) | Mitigation (for survival) No interaction (for reproductive behavior) |

| | | | | | | | | |
|----|--------------------|---|---------------------------------------|--|--|--|----------------------|--------------|
| | | | | | | reduction of Pb effects by parasitism. However, no coefficient estimates were shown. Breeding propensity and clutch size negatively related to blood Pb in anti-parasitism treated and control groups. | | |
| 13 | Lunny et al. 2020 | Killdeer (<i>Charadrius vociferous</i>) | Movement, Foraging, Personality | PCBs 0 µg PCB-126/ml (DMSO only), 15 ng/g egg (30 µg PCB-126/ ml; nominal = 44 µg/ml) or 41.5 ng/g egg (83 µg PCB-126/ml; nominal = 89 µg/ml) | Temperature 36, 37.5, or 39°C | Chicks exposed to PCBs in ova displayed faster righting reflexes when incubated at 39°C as compared to unexposed chicks incubated at 36°C. Thus, PCBs had an enhanced effect on righting responses at higher temperature, suggesting exacerbation of PCB toxicity. | Synergy/ Emergent | Exacerbation |
| 14 | Zabala et al. 2020 | Great egret (<i>Ardea albus</i>) White ibis (<i>Eudocimus albus</i>) | Reproductive I | Metal: Hg Treatment groups: 0, 0.05, 0.1, 0.3 ppm MeHg in food. Wild: Range of 5.26–19.34 mg/g dw total Hg in nestling feathers. | Food availability, weather conditions | Low food availability and Hg contamination on the population scale additively reduced breeding numbers in great egret. However, effect of Hg on breeding numbers was greater for great egrets in the field, than for white ibis in the laboratory, suggesting possible synergistic | Synergy | Exacerbation |

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|----|---------------------|--|-----------------------|---|---------------------------|--|----------------------|---|
| | | | | | | effect of Hg combined with the challenges of multiple stressors encountered in the field. | | |
| 15 | Esparza et al. 2022 | Thick-billed murre (<i>Uria lomvia</i>) | Movement, Foraging | Metal: Hg POPs: OCs Mean \pm SE (range): tHg: 1.51 ± 0.05 (0.81-2.74) $\mu\text{g/g dw}$ ΣPCBs : 0.01 ± 0.001 (0.001, 0.02) $\mu\text{g/g ww}$ DDE: 0.004 ± 0.0003 (0.0007, 0.01) $\mu\text{g/g ww}$ HCB: 0.004 ± 0.0002 (0.003, 0.01) $\mu\text{g/g ww}$ | Timing of sea ice breakup | Hg exposure level influenced triiodothyronine (T3) levels only in years in which sea ice retreat was early, and foraging conditions were poor. However, the direction of the effect was positive in a year with moderately advanced sea ice breakup, and negative in a year with strongly advanced sea ice breakup. Increased T3 levels were in turn associated with reduced time spent underwater, engaged in energetically intensive diving behavior. Thus, early sea ice breakup led to emergent relationships between T3 and Hg, and T3 and time underwater. However, interactive effects of Hg were indirectly mediated through the | Synergy/ Emergent | Exacerbation (but mediated through physiology) |

| | | | | | | | | |
|----|--------------------|---|--|--|---|---|----------|--------------|
| | | | | | | physiological effect, with no statistically significant direct effect of Hg on behavior. | | |
| 16 | Smith et al. 2022 | Common eider (<i>Somateria mollissima</i>) | Reproductive I and II | Metal: Hg tHg, Mean \pm SE (range): 1.12 \pm 0.44 (0.31–2.72) μ g/g dw in egg homogenate | Temperature | When temperatures were warm, females with low Hg laid eggs later and had more incubation interruptions compared to contaminated females. Thus, a reduced response to temperature was observed in contaminated females. | Antagony | Inhibition |
| 17 | Grunst et al. 2023 | Little auk (<i>Alle alle</i>) | Movement, Foraging Reproductive II | Metal: Hg tHg, Mean \pm SE (range): | Sea surface temperature (SST), Sea ice coverage (SIC) | Birds highly contaminated with Hg took longer inter-dive breaks than less contaminated birds, but only when making long dives (Beta coefficient for interactive effect = 6.70 \pm 2.99). Dive durations increased with SST, suggesting that behavioral effects could be accentuated in warming oceans. | Synergy | Exacerbation |

Abbreviations: Hg: mercury, tHg = total mercury, MeHg =methymercury, Pb = lead, POPs: persistent organic pollutants (includes OCs), OCs: organochlorines (includes PCBs, OCPs, HCB), PCBs: polychlorinated biphenyls, OCPs: organochlorine pesticides (DDT, CHL etc.), DDT: dichlorodiphenyltrichloroethane, DDE: dichlorodiphenyldichloroethylene, HCB: hexachlorobenzene, CHL: chlordanes, PBDEs: polybrominated diphenyl ethers (a legacy brominated flame retardant), HCB: hexachlorobenzene, CORT: corticosterone, PRL: prolactin. *Behavioral change indirectly inferred from reproductive outcomes. *Contaminant concentrations reported within the control group for one study year (2000). Concentrations were similar in other group-years

4. Behavioral reaction norm-based conceptual framework. Based on our review, we developed a conceptual framework to better understand contaminant-by-environment interactive effects on animal behavior from a behavioral reaction norm perspective. The central tenet of our framework is that contaminant-by-environment interactive effects on animal behavior arise when behavioral reaction norms are nonparallel when comparing individuals differing in contaminant exposure (or exposure to another stressor) when moving along gradients in other stressors (or contamination) (Fig. 1). This idea can be illustrated within a general (or generalized) linear modelling framework with an interactive effect, expressed as $y(\mu) = \beta_0 + \beta_1x_1 + \beta_2x_2 + \beta_{12}x_1x_2$. In this model, the interactive effect (β_{12}) alters the response to x_2 , (β_2) as a function of x_1 (and vice versa), as can be visualized by rewriting the model equation as $y(\mu) = \beta_0 + \beta_1x_1 + (\beta_2 + \beta_{12}x_1)x_2$ (Gennings et al. 2005). In contrast, given parallel behavioral reaction norms, effects are additive rather than interactive, with behavioral changes across gradients in one stressor not varying as a function of exposure to others (non-horizontal gray surfaces in Fig. 1). Note that behavioral reaction norms need not be linear for these concepts to apply. Thus, in the graphical representation of our framework, we have used non-linear behavioral reaction norms, to more realistically capture expectations for patterns of behavioral plasticity (Fig. 2). We identified four general patterns in non-parallel behavioral reaction norms which could underlie contaminant-by-environment interactive effects: exacerbation (Fig. 2a), mitigation (Fig. 2b; Fig. 2e), inhibition (Fig. 2c), and convergence (Fig. 2d). Figure 3 provides graphical, empirical examples of exacerbation and inhibition, using studies identified in our review.

Conceptualizations of multiple stressor interactive effects have generally taken an additive model as the null model (although alternative null models are sometimes required; Dey and Koops 2021), and described effects as antagonistic (less than additive) or synergistic (more than additive) (Crain et al. 2008; Wilson et al. 2020; Fig. 2f). However, when effects of multiple stressors are in opposing directions, distinguishing antagonism versus synergy becomes more complex, which has led to discrepancies among

classification systems (Crain et al. 2008; Piggott et al. 2015; Wilson et al. 2021; see Fig. 2f for clarification).

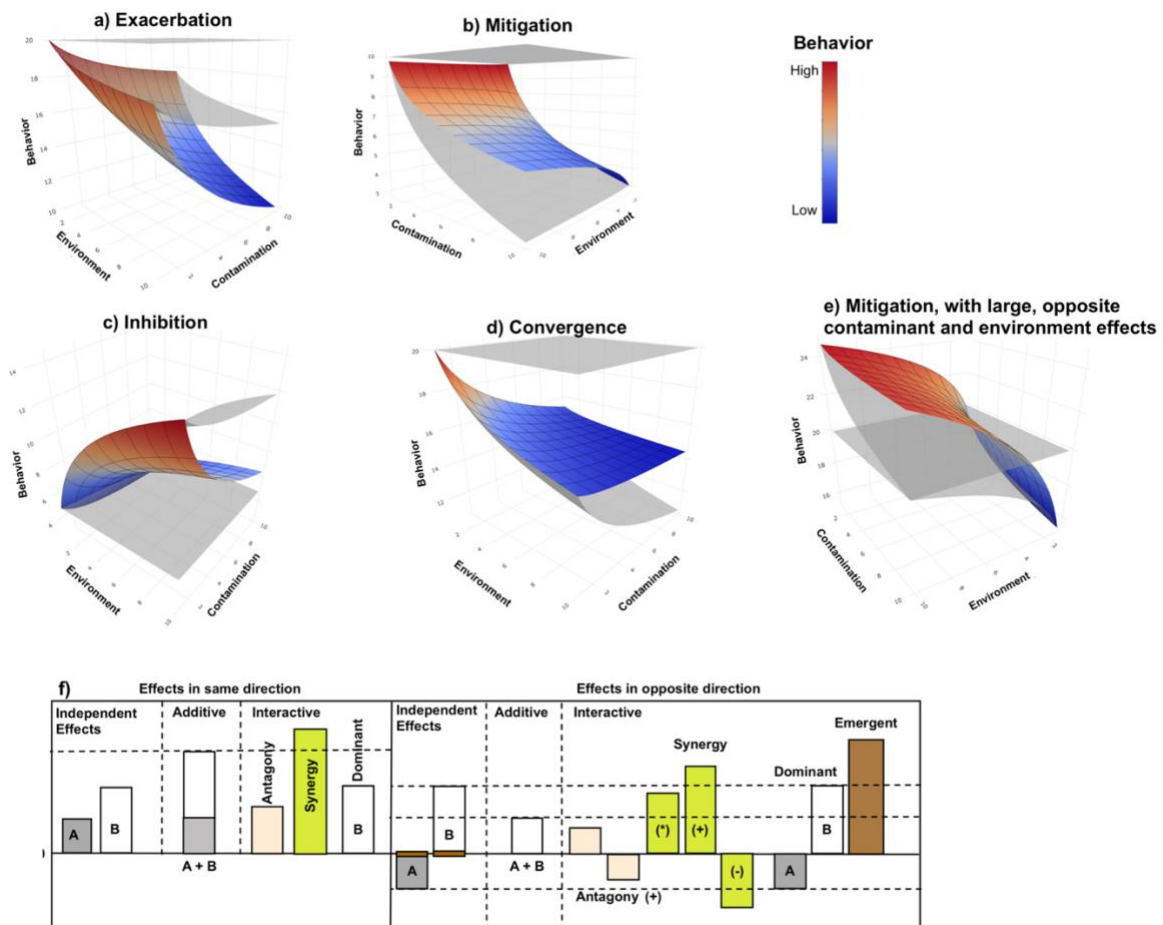


Figure 2. Patterns in three-dimensional (3D) behavioral reaction norms which may underlie interactive effects of contamination and environmental factors on behavior. The colored surfaces represent 3D reaction norms incorporating interactive effects, with lines within the colored planes representing behavioral reaction norms of individuals differing in contamination (or exposure to the other environmental stressor) along a gradient in the other stressor (contamination, or the other stressor). Non-horizontal gray surfaces are additive predictions (reaction norms parallel between individuals differing in contamination or environmental status). The horizontal gray plane delineates the level of baseline behavior, to facilitate visualization of behavioral changes across the range of conditions. When the colored surface is between the additive prediction surface and baseline plane, antagonism is entailed (change from baseline less than additive), whereas when the colored surface is above or below both the additive and baseline surfaces, synergy is entailed. The surfaces were generated using linear models with log transformation of the predictor variables (contamination and environment) to generate non-linearity. After the name of each pathway, we indicate in parentheses the magnitude of the contamination (C), environment (E), and interactive (I) effects which were used to produce the plots. (a) Exacerbation ($C = -1$, $E = -1$, $I = -1$), steeper behavioral reaction norms in highly contaminated (or otherwise stressed) individuals, leading to synergistic behavioral changes and divergence of behavioral patterns between individuals differing in contamination/environmental status. (b) Mitigation ($C = -3.5$, $E = -0.1$, $I = 0.7$), steeper reaction norms in highly contaminated individuals lead to convergence of behavioral patterns, and antagonistic effects on behavioral change. (c) Inhibition ($C = -1$, $E = 4$, $I = -1$), dampened reaction norms in highly contaminated individuals lead to antagonism of behavioral changes. (d) Convergence ($C = -2$, $E = -2$, $I = 0.7$), steeper reaction norms in less contaminated (or otherwise less stressed) individuals associated with convergence of behavioral patterns between individuals differing in contamination/environmental status. (e) Mitigation with large, opposite effects of contamination and the additional environmental stressor ($C = -2$, $E = 2$, $I = 0.7$), in which case a pattern of mitigation

(steep behavioral reaction norms in highly contaminated individuals converging on shallower reaction norms in less contaminated individuals) can also lead to synergy in some regions of the environmental gradient. The same is true for inhibition. Note that graphs representing mitigation are viewed from a different perspective than the other graphs, to facilitate viewing. (f) Classification of interactive effects according to standard multiple-stressor terminology, when individual stressors are in the same versus opposite directions. We have used this classification system to determine whether the pathways comprising our framework generate synergy vs. antagonism.

Moreover, these classifications have been developed in the context of factorial experiments, rather than continual environmental gradients. In light of these considerations, our framework offers a complementary approach to understanding interactive effects of multiple stressors on behavior, and points out non-equivalent patterns in behavioral reaction norms through which antagonistic effects on patterns of behavioral change can arise. Below we describe the four patterns in detail.

First, exacerbation reflects aggravation of toxicological effects by additional stressors (and/or vice versa), and generates synergy, as the reaction norms of more and less contaminated individuals diverge across gradients in other stressors (Fig. 2a). Given exacerbation, highly contaminated (or otherwise more stressed) individuals display larger magnitude behavioral changes (steeper reaction norms) when exposed to additional stressors as compared to uncontaminated counterparts, which better maintain behavioral patterns across conditions. This pattern predominated in our review, being observed in 10 of 13 studies that reported evidence for contaminant-by-environment interactive effects. To remind the reader of one such example, glaucous gulls highly exposed to OCs provisioned chicks at lower rates than less contaminated birds when feeding on fish and faced with high flight costs, but not when foraging on bird eggs and faced with lower costs. Thus, contaminated birds appeared unable to maintain provisioning performance when faced with increasing foraging challenge, generating steeper behavioral reaction norms across environmental gradients in foraging costs in contaminated as compared to less contaminated individuals (Fig. 3a). Anthropogenic environmental change is projected to increase foraging challenges for many species, across diverse ecosystems, by transforming resource bases and foraging conditions. For instance, our study on little auks demonstrated that birds dive deeper and longer as SST warms, likely reflecting changes in copepod prey distribution (Grunst et al. 2023). Exacerbation of the behavioral

ramification of contamination due to foraging challenges is predicted to become increasingly prevalent under global change scenarios.

Second, like exacerbation, mitigation entails steeper behavioral reaction norms in more contaminated as compared to less contaminated individuals. However, in the case of mitigation, the behavioral reaction norms of more and less contaminated individuals converge upon increasing exposure to a second stressor (Fig. 2b), suggesting reduction of toxicological effects by another stressor. Whereas exacerbation generates synergy, mitigation (and the other pathways discussed below) will commonly generate antagonism (Fig. 2b). However, if both the contamination and environment effects are relatively strong, dynamics become more complex, and a pattern of mitigation might also generate synergistic effects on behavioral change in some portions of multi-stress space (Fig. 2e). In our review, the study involving effects of Hg contamination and parasitism on common eiders suggested a pattern of mitigation. Parasites appeared to cause survivorship of individuals highly exposed to Hg to match those of less exposed counterparts, perhaps through effects on behavioral or physiological capacity (Morrill et al. 2019).

Third, inhibition occurs when contamination (or another stressor) dampens behavioral reaction norms with respect to additional stressors, such that contaminated individuals show limited behavioral plasticity in responses to environmental change, and behavioral patterns of individuals differing in contamination status diverge (Fig. 2c). In our review, the study involving effects of Hg-contamination on the incubation patterns of common eiders under varying temperatures tentatively suggested inhibition, as females with high egg-Hg levels displayed less behavioral plasticity in incubation rhythms with temperature (Smith et al. 2022; Fig. 3b). Inhibition involves antagonistic effects of contamination on behavioral responses to additional environmental stressors. However, synergistic effects on fitness variables might result, as behavioral changes (e.g. increased foraging effort) can buffer higher level traits against perturbation (e.g. Grémillet et al. 2012). Furthermore, as for mitigation (see Fig. 2e), given strong, opposing contamination and environment effects, a pattern of inhibition can also generate synergistic effects on behavioral changes in some portions of multi-stress space. Under scenarios of global change that threaten resource bases and alter thermal conditions, behavioral plasticity might become increasingly important to buffering

individual fitness and stabilizing populations, for instance, if increases in foraging range become necessary to maintain resource intake and chick provisioning rates (Jakubas et al. 2017). Thus, effects of contaminants on the capacity for behavioral plasticity could become increasingly problematic. However, evidence for such effects remains extremely limited (only one possible example identified in our review).

Fourth, convergence occurs when steeper behavioral reaction norms in less contaminated (or otherwise less stressed) individuals exposed to additional stressors cause reaction norms of more and less exposed individuals to converge (Fig. 2d). This type of effect was observed in the study involving great egrets, in which birds contaminated with Hg displayed greater latency to capture prey when prey detectability was high, but not when prey detectability was reduced (Bouton et al. 1999). Behavioral reaction norms in predatory behavior could converge with declining prey detectability or abundance, given that all individuals may be unable to maintain high rates of prey pursuit and capture when prey becomes too difficult to locate. Conversely, as prey abundance increases, less contaminated predators might display greater positive functional responses, causing diverging behavioral patterns when moving towards the more permissive foraging environment (Pirotta et al. 2022). Convergence generates antagonistic effects on behavioral changes, and antagonistic effects on changes in fitness traits are also predicted, as behavioral patterns become more similar among individuals differing in contamination status. However, in contrast to mitigation, implications for population stability might not be positive, as this form of antagonism involves approach of less contaminated (or otherwise less stressed) individuals to performance levels of highly contaminated individuals, rather than vice versa.

We envision that feedbacks could also occur between exacerbation, inhibition, mitigation and convergence effects, and between effects operating within different behavioral domains. For instance, failure of contaminated individuals to increase foraging activity in response to resource scarcity (inhibition) could cause deteriorating body condition, release of contaminants from lipids (exacerbation), and further reductions in foraging capacity (feedback) (Peterson et al. 2018), preventing maintenance of offspring provisioning (exacerbation) (Bustnes et al. 2005). Moreover, feedbacks might occur between diverse physiological pathways that might underlie contaminant-by-environment interactive effects on

behavioral reaction norms (see Box 1 for a discussion of potential underlying physiological mechanisms). For instance, endocrine disruption might affect energy balance via effects on the hypothalamus-pituitary-adrenal (HPA) and thyroidal (HPT) axes, which regulate energy homeostasis (Sapolsky et al. 2000; Blévin et al. 2017). Energy balance could in turn feedback to affect endocrinology, as fasting and negative energy balance promote elevated glucocorticoids and declines in thyroid hormones (Wingfield et al. 1998; Fekete and Lechan 2014).

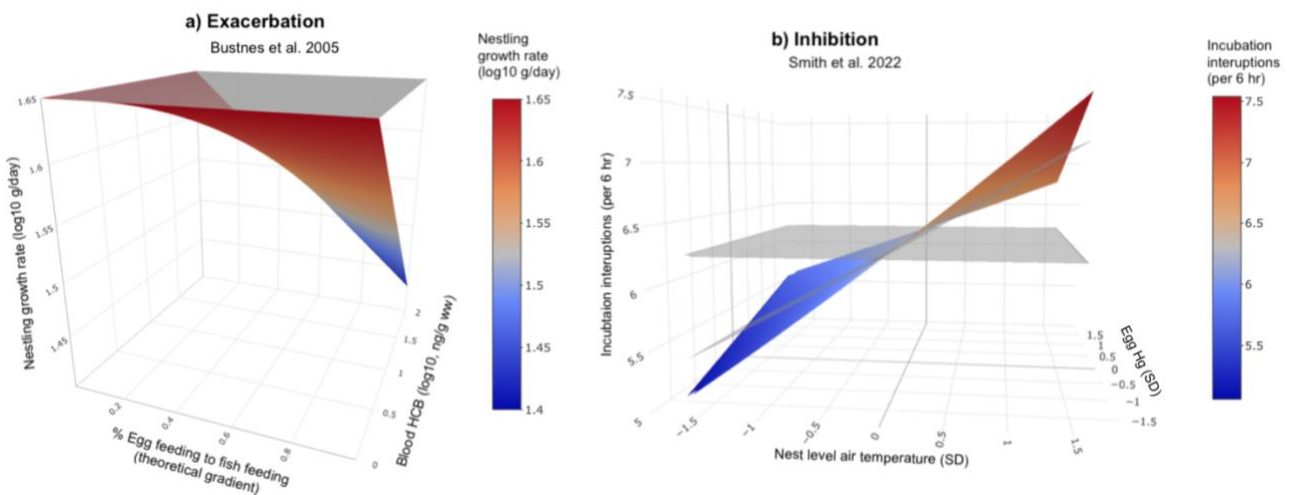
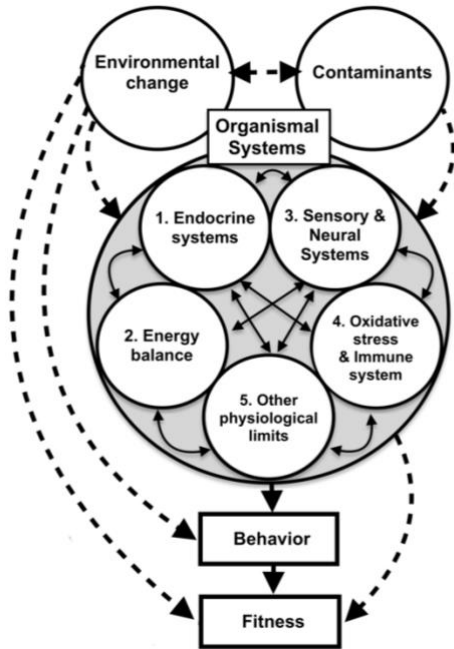


Figure 3. Empirical example of a) Exacerbation and b) Inhibition from the avian behavioral ecotoxicological literature, with graphical representations generated using reported coefficient estimates. The slanted gray plane is the additive prediction, and the horizontal gray plane delineates the level of baseline behavior, with these two planes equivalent and both horizontal in (a). Coefficient estimates underlying the represented surfaces were for Bustnes et al. (2015): Intercept = 23.99, Contamination = -1.38, Treatment (Environment) = 32.43 (control), 0 (fed), Interaction = -5.58 (control), 0 (fed), and for Smith et al. (2022): Contamination = 0.003, Temperature = 0.11, Interaction = -0.025. In the exacerbation example (a), a linear relationship between blood hexachlorobenzene (HCB) concentrations and chick growth rates was observed for female glaucous gulls (*Larus hyperboreus*) feeding on fish, for which flight costs were high, but not for females feeding on bird eggs, for which flight costs were low. The x-axis represents a theoretical gradient, ranging from 0 to 100% fish feeding behavior. In the inhibition example (b), incubating common eiders (*Somateria mollissima*) with low mercury (Hg) contamination levels increased the frequency of incubation interruptions with temperature more than less contaminated females. Here, the use of standardized and centered variables changes the baseline level to the mean. Thus, the additive prediction (slanted gray plane) passes through the center (z = model intercept, $x = 0$, $y = 0$) of the colored plane representing model predictions, and predicted reaction norms of all individuals cross at this point. Birds with high levels of Hg-contamination have predicted values between the baseline plane and additive prediction for both high and low temperature, indicating behavioral changes lesser in magnitude than the additive prediction, and antagonism of the behavior response to temperature variation.

Box 1. Possible physiological mechanisms underlying contaminant-by-environment interactions:

1. *Endocrine system* The endocrine system, including the hypothalamus-pituitary-adrenal (HPA), -gonadal (HPG), and -thyroidal (HPT) axes might play a central role in mediating exacerbation of toxicological effects of contaminants within stressful environments. Physiological stress responses mediated by the HPA axis,

catecholamines, and cytokines maintain organismal homeostasis in challenging environments (the concept of



allostasis; McEwen and Wingfield 2003). Unpredictable environmental stressors, such as food shortage and human disturbance, may combine with contamination to lead to allostatic overload (McEwen and Wingfield 2003), which is associated with increases in GCs, suppression of the HPG axis and reproductive hormones (prolactin, testosterone, etc.), and pathology (McEwen and Wingfield 2003). Thus, behavioral changes involving HPA regulation might only emerge in contaminated individuals after thresholds in environmental stress are surpassed. The HPT and HPG axes are also highly sensitive to endocrine disruption and environmental conditions, such as resource availability and thermal stress, such that exacerbation might be mediated through these axes (Wingfield and Mukai 2009; Blévin et al. 2017). Given the HPT axis' pivotal role in regulating metabolism, energy balance, and thermoregulation, contaminant effects on the HPT axis could be especially important to mediating exacerbation effects involving

maintenance of energetically intensive behaviors under conditions of resource shortage or thermal stress (Blévin et al. 2017; Esparza et al. 2022). Furthermore, behavioral plasticity involves translating environmental cues into hormonal changes that regulate behavioral shifts (Wingfield and Mukai 2009; Hau and Goymann 2015). Thus, endocrine disrupting effects of contaminants might limit behavioral responses to environmental cues, generating inhibition. For example, suppression of adrenocortical stress responses, as found in tree swallows (*Taeniopygia guttata*) exposed to polychlorinated biphenyls (PCBs) (Franceschini et al. 2008), could prevent behavioral changes mediated by GCs, such as increased foraging effort (Angelier et al. 2007). Similarly, thyroid dysregulation, as found in thick-billed murrelets (*Uria lomvia*) exposed to PFASs, could prevent upregulation of energetically expensive behaviors, such as diving or incubation, by interfering with bioenergetics (Choy et al. 2022, Esparza et al. 2022).

2. Energy balance Energetic challenges caused by environmental change and contamination might interact to disrupt energy balance and induce behavioral changes in contaminated individuals, generating exacerbation. Contamination can impair metabolism and thermoregulation (Sokolova 2004; Gerson et al. 2019) and compromise energy intake by reducing foraging and assimilation efficiency (Bustnes et al. 2003; Li and Xie 2019), and might thereby compound energetic challenges caused by environmental change, such as change in spatiotemporal resource distribution (Visser et al. 1998; Grémillet et al. 2012), or elevated thermoregulatory and immunological costs (Riddell et al. 2019; Mills et al. 2010). Moreover, contaminated individuals might be unable to adopt energetically expensive behaviors to cope with environmental change, generating inhibition. For example, contaminated individuals might be unable to increase foraging effort in response to redistribution of resources, due to poor body condition (Ackerman et al. 2019) or disrupted metabolism (Blévin et al. 2017).

3. Sensory and neural systems Reduced sensory or cognitive capacity in contaminated individuals might have larger behavioral effects in challenging

environments, generating exacerbation. For instance, reduced problem-solving capacity might become more problematic given novel foraging problems, as encountered in urban environments (Sol et al. 2005). Furthermore, neurotoxicological effects of contaminants might prevent contaminated individuals from learning to perform new behaviors as conditions change, causing inhibition (Burger and Gochfeld 2005).

4. Oxidative stress and immune function Toxicological effects of contaminants on oxidative stress (e.g. diverse metals: Koivula and Eeva 2010; POPs and Hg: Costantini et al. 2014) and the immune system (e.g. Teitelbaum et al. 2022) might be exacerbated under environmental conditions that limit energy allocation towards antioxidant and immune defenses (e.g. resource shortage), or render contaminants more toxic (e.g. increasing temperature) with ramifications for behavioral patterns. High levels of oxidative stress or infection by pathogens in contaminated individuals might also inhibit behavioral plasticity (e.g. changes in activity patterns, increases in dive length) in response to additional environmental stressors by leading to biomolecular and tissue damage and thereby limiting behavioral performance capacity.

5. Other physiological limits Other physiological limits associated with contamination might also contribute to forcing behavioral changes in response to additional environmental stressors, causing exacerbation. For example, effects of contaminants on oxygen carrying capacity (Olsen et al. 2000), metabolic scope (Gerson et al. 2019), or wing symmetry (Bustnes et al. 2002; Evers et al. 2008) might have larger effects on movement behavior under challenging thermal or wind conditions. Such physiological limits might also constrain behavioral plasticity, generating inhibition. For instance, poor oxygen carrying capacity (Olsen et al. 2000) might prevent increases in dive depth if prey distributions shift deeper in warming oceans (Nye et al. 2009).

Our framework is primarily conceptual rather than mathematical, involving different general patterns in behavioral reaction norm shape. However, in Table 2, we indicate which signs of effects are predicted for the contamination, environment, and interaction effect in a general linear model (GLM) framework given each pattern (exacerbation, mitigation, inhibition, convergence), to aid researchers in interpreting statistical results within the context of our framework. Furthermore, we indicate whether synergy, antagonism or emergent effects are expected within the framework of factorial experimental designs. Note that mitigation and inhibition are mathematically equivalent within a GLM framework, except that one involves antagonism of a strong contaminant effect, and the other antagonism of a strong environment effect.

Importantly, neither exacerbation nor inhibition necessarily involves maladaptive behavior by highly contaminated individuals, since what constitutes an adaptive response to environmental stressors will often differ as a function of contamination status. For instance, highly contaminated individuals may have more constrained energy budgets (English et al. 2021), be less able to escape predators (Kobiela et al. 2015), or adopt distinct life history strategies (Fritsch et al. 2019). Thus, exacerbation could involve

adaptive shifts in life history strategy by highly contaminated individuals in response to new conditions. Moreover, contamination could inhibit non-adaptive, as well as adaptive, behavioral responses, by antagonizing physiological effects of additional stressors, or imposing constraints. For instance, behavioral responses to frequent human disturbances that pose little true threat could be suppressed in contaminated individuals due to poor energy balance, promoting the erroneous conclusion that these individuals have habituated to disturbance (Beale and Monaghan 2004).

We would also like to emphasize that our pathways are complementary, rather than equivalent to, those of climate change (environment)-induced toxicant sensitivity versus toxicant-induced climate change (environment) sensitivity, outlined in recent reviews (Hooper et al. 2013; Alava et al. 2017), and referenced by a growing number of empirical studies (e.g. Hallman and Brooks 2016; de Beeck et al. 2018). Exacerbation can involve either environment-induced toxicant sensitivity (i.e. $C = 0$ in Table 2), toxicant-induced environment sensitivity (i.e. given $E = 0$ in Table 2), or both simultaneously (i.e. $C \neq 0$ & $E \neq 0$ in Table 2). In fact, defining an effect as either environment- or contaminant-induced can often seem paradoxical, given that synergistic interactions are often predicted to involve simultaneous magnification of both effects. Inhibition might prove an important pathway underlying toxicant-induced environment sensitivity, by limiting behavioral responses to additional environmental stressors.

Table 2. Expected direction of independent and interactive (C = contaminant, E = environment, I = interactive) effects in a GLM, and possible mathematical forms of effects in a factorial experimental design (Syn. = synergy, Ant. = antagony, Emerg. = emergence) for exacerbation, mitigation, inhibition and convergence. Mitigation and inhibition are distinguished by whether the interactive effect is antagonistic with respect to the contamination effect (mitigation) or the effect of the other environmental stressor (inhibition). If the contaminant and environment effects are large and predominant for mitigation and inhibition, respectively, then these pathways are discrete and both produce a pattern of antagony. However, if the contamination and environmental effects are both large, dynamics become more complex, and patterns of synergy will be generated in some regions of environmental space, once the antagonized stressor's effect has been completely reversed (see Fig. 1e). Furthermore, if the interactive effect is large relative to main effects, a pattern of exacerbation/synergy will predominate regardless of the directions of main effects.

| Pathway | Independent & Interactive effects | | | Mathematical form | | |
|---------------------|-----------------------------------|---|---|-------------------|------|--------|
| | C | E | I | Syn. | Ant. | Emerg. |
| Exacerbation | - | - | - | × | | |
| | + | + | + | × | | |
| | - | 0 | - | × | | |
| | + | 0 | + | × | | |
| | 0 | - | - | × | | |

| | | | | | |
|--------------------|-----------|-----------|---|---|---|
| | 0 | + | + | × | |
| | 0 | 0 | - | | × |
| | 0 | 0 | + | | × |
| Mitigation | - (large) | +/- | + | × | × |
| | + (large) | +/- | - | × | × |
| | - | 0 | + | | × |
| | + | 0 | - | | × |
| Inhibition | +/- | + (large) | - | × | × |
| | +/- | - (large) | + | × | × |
| | 0 | + | - | | × |
| | 0 | - | + | | × |
| Convergence | - (large) | - (large) | + | | × |
| | + (large) | + (large) | - | | × |

To date, the avian behavioral ecotoxicological literature provides limited evidence for inhibition, mitigation and convergence (only one study each), perhaps reflecting the dearth of studies that have adopted a multiple stressor perspective and considered interactive effects. To motivate further research, we proceed to draw on our literature review to suggest possible ways in which documented effects of contamination on behavior might: (1) be exacerbated by environmental change, and (2) inhibit responses to environmental change, across behavioral domains in which toxicological effects of contaminant exposure have been documented (e.g. Fig. 4). We also suggest possible mitigation and convergence effects, but focus on exacerbation and inhibition.

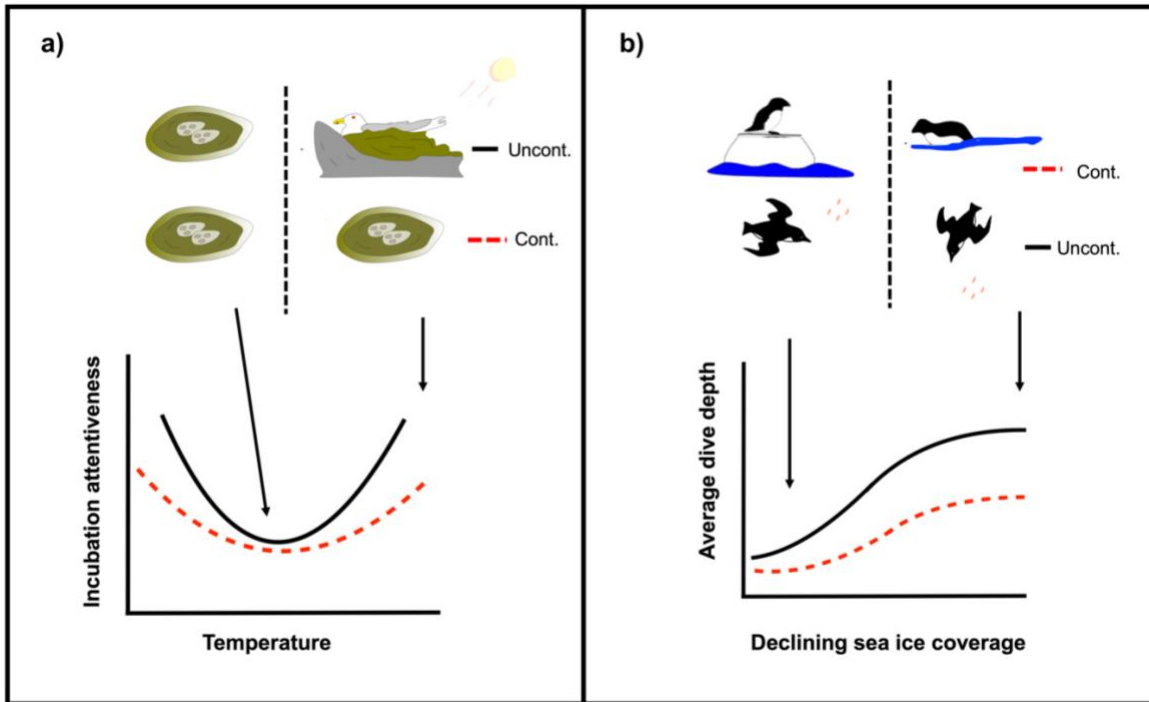


Figure 4. Theoretical examples of inhibition in two behavioral domains. (a) During incubation, uncontaminated birds might increase attentiveness during extreme temperatures to protect eggs, whereas contaminated individuals may be unable to do so. (b) During foraging, uncontaminated birds might increase dive depth or duration in response to changing prey distribution, for instance due to changing sea ice coverage (Amélineau et al. 2019). Contaminated birds might be unable to do so, for instance due to low hemoglobin levels resulting in reduced oxygen carrying capacity (Olsen et al. 2000).

5. Possible contaminant-by-environment interactive effects across avian behavioral domains from a behavioral reaction norm perspective

5.1. Reproductive behavior I: Decision to nest, phenology, and sexual display: Due to their central importance to fitness, reproductive behaviors have been the focus of a predominance of avian behavioral ecotoxicological studies. Thus, substantial evidence for effects of contaminants on behaviors spanning avian reproductive cycles exists (Table S1). We propose that early in the reproductive cycle environmental stress associated with global change could exacerbate documented negative effects of contaminants on skipping breeding (e.g. Tartu et al. 2013) and sexual display behaviors, such as song

(Gorissen et al. 2005). For instance, common murre breeding in the North Sea skip breeding at higher proportions after winters when sea surface temperature (SST) is high, due to negative effects on prey availability (Reed et al. 2015), and this effect could be exacerbated in contaminated birds with disrupted endocrinology and energetics (Tartu et al. 2015b; Goutte et al. 2018). Environmental change could also exacerbate delays in egg laying date which have been documented in contaminated females (Helberg et al. 2005, Bustnes et al. 2007), especially by threatening energy balance. However, contaminant exposure has also been associated with advances in egg laying date in some cases, for instance in great tits (*Parus major*) exposed to perfluoroalkyl acids (PFAAs) (Groffen et al. 2019).

Endocrine disrupting and energetic effects of contamination might also inhibit adjustments of reproductive phenology and sexual display behavior to environmental conditions. Of particular concern, contamination could inhibit advances in the timing of breeding and egg laying, which might otherwise allow birds to track climate change-associated shifts in spring phenology (Nussey et al. 2005). Indeed, contaminant burdens have often been related to body condition in birds (e.g. Hg; Ackerman et al. 2019), and body condition constrains initiation of egg laying (Provencher et al. 2017).

5.2. Reproductive II: Parental care: Contamination can disrupt avian parental behaviors, including incubation (e.g. Hartman et al. 2019), nest defense (e.g. Goutte et al. 2018) and parental provisioning (e.g. Halbrook and Arenal 2003) (Table S1). These effects are often negative (Fig. 1), and could be exacerbated under challenging environmental conditions, as indeed documented by several studies (Bustnes et al. 2005; 2015; Goutte et al. 2018; Table 1), especially as parental behaviors are energetically demanding (Golet et al. 2000; Weimerskirch et al. 2003) and sensitive to endocrine disruption (Tartu et al. 2014, 2015a). Incubating birds nesting in open areas are exposed to climatic extremes for extended periods without feeding, deeming them vulnerable to heat stress and disruption of energy balance (Oswald and Arnold 2012). Furthermore, incubation fasting releases contaminants from lipid reserves, amplifying toxicological effects, particularly given resource shortage (Marteinson et al. 2016). Especially in cooler climates, warming temperatures could also reduce effects of contamination on incubation by

easing thermoregulatory demands. However, in this case, warming temperature does not act as a stressor, but rather ameliorates thermal stress. Moreover, phenological mismatches between nestling periods and resource peaks caused by climate change (Visser et al. 1998; Gaston et al. 2009), and spatial shifts in resource availability, might amplify foraging challenges, threatening the capacity of contaminated birds to maintain parental performance (Bustnes et al. 2005; 2015). For instance, Arctic seabirds that specialize on sea-ice associated prey often have to fly farther from colonies to reach profitable foraging grounds as sea ice recedes due to climate change (Jakubus et al. 2017), which could lead to decreases in parental provisioning in contaminated birds with limited energy budgets.

In addition, contamination could reduce the scope for adjusting parental effort to environmental change, generating inhibition. For instance, nest predation in shorebirds has increased worldwide over the past 70 years due to climate change, especially in the Arctic (Kubelka et al. 2018). Nest predation pressure favors increased nest attentiveness (Fontaine and Martin 2006; Meyer et al. 2020), which contaminated birds might be unable to sustain. Changing resource bases might also favor increased offspring provisioning effort. For instance, common murre (*Uria aalge*) can increase foraging effort by 2 hr per day to maintain chick provisioning rates given low prey density (Harding et al. 2007). We propose that such costly increases in parental effort could be inhibited by energetic, physiological and hormonal constraints associated with contamination.

5.3. Movement, foraging and migration: Large- (i.e. migration) and smaller-scale movement patterns and behavioral performance traits central to foraging and migration (prey capture efficiency; flight speed) are sensitive to neurotoxic, energetic and endocrine-disrupting effects of contaminants. For example, foraging golden eagles (*Aquila chrysaetos*) travelled shorter distances and flew at reduced heights when exposed to blood Pb concentrations as low as 25 ppb (Ecke et al. 2017), and migrating white-crowned sparrows (*Zonotrichia leucophrys*) exposed to a neonicotinoid extended stopover duration (Eng et al. 2019). Activity patterns are central to energy budgets in free-living animals (Wilson et al. 2020), and energetic and physiological costs of activity depend on environmental conditions. For instance, costs of

flapping flight increase with head winds and high temperatures (Elliot et al. 2014; Nord and Nilsson 2018). Thus, changes in environmental conditions have the potential to exacerbate effects of contaminants on movement patterns during foraging and migration, rendering individuals with impaired physiology or energy balance unable to maintain behavioral patterns. In addition, deficits in foraging efficiency associated with neurotoxic effects of contaminants could be exacerbated given reduced prey density or detectability. However, contrary to this hypothesis, reduced foraging efficiency in Hg-exposed white ibis (Adams and Frederick 2008) and great egrets (Bouton et al. 1999) was not exacerbated when prey detectability was reduced. Rather, as aforementioned, differences in foraging performance between Hg-exposed and unexposed great egrets were greater when prey detectability was high (Bouton et al. 1999). Thus, contaminant exposed birds could be unable to capitalize on permissive foraging conditions, such that convergence effects occur given deterioration of foraging landscapes.

Contamination could also inhibit plasticity in foraging patterns and migratory timing, which can otherwise allow animals to adjust to changes in resource distributions and spring phenology, respectively (Both and Visser 2001; Grémillet et al. 2012, Conklin et al. 2021). For instance, little auks in East Greenland appear to shift to deeper dives in the absence of sea ice, perhaps tracking copepod distributions (Amélineau et al. 2019). We predicted that birds highly contaminated with Hg might be unable to do so due to reduced oxygen carrying capacity (Olsen et al. 2000; Fig. 4b). However, this prediction was not supported by our recent empirical study on little auks. Rather, highly contaminated birds increased inter-dive intervals when making long dives, but did not show shorter dive lengths (Grunst et al. 2023).

In addition, birds adjust migratory phenology according to conditions at wintering and stopover sites, via effects of environmental cues on the neuroendocrine system (Ramenofsky and Wingfield 2007, Haest et al. 2020; Conklin et al. 2021). Contaminant exposure could combine with other environmental constraints to limit plasticity in migratory timing, for instance by reducing refuelling efficiency (Eng et al. 2019). Due to high rates of energy intake and expenditure, migrating birds intake and release contaminants from lipid reserves at high rates, increasing sensitivity to contamination (Ma et al. 2018).

5.4. Cognition and personality: Cognition is the process by which animals integrate, store and adjust behavior to environmental information (Swaddle et al. 2017; Cauchoux et al. 2020), whereas animal personality is defined by consistent among individual differences in behavioral traits, such as aggressiveness and neophobia, which affect how animals interact with the environment and balance life-history tradeoffs (Sih et al. 2004; Wolf et al. 2007). Cognition and personality are both sensitive to contaminants. For example, great tits with elevated blood Pb levels explored a novel environment more slowly (Grunst et al. 2019a), and PCB exposure impaired learning in starlings (Zahara et al. 2015).

Endocrine disrupting effects of contaminants might alter how the HPA and HPG axes respond to additional environmental stressors (Tartu et al. 2015a, Montiglio and Royauté 2014). Consequentially, stressful environments could exacerbate contaminant-related differences in personality traits that are hormonally-mediated, generating synergies (Hau and Goymann 2015). Furthermore, effects of contaminants on cognitive performance could be exacerbated under environmental conditions that cause stress or distraction, such as traffic noise (Osbrink et al. 2021). Interactions between contamination and environmental stressors, such as food shortage or heat stress, could also exacerbate neurotoxic effects on the development of personality and cognitive traits, as found in killdeer (Lunny et al. 2020; Table 1).

Contamination could also inhibit plasticity in personality and cognitive traits through endocrine disruption or neurotoxicity. Animal personality requires limits to plasticity to maintain among individual behavioral differences across contexts (Sih et al. 2004). However, individuals nonetheless display some adjustment of personality traits to environmental conditions. For instance, urban animals can become less neophobic and bolder towards humans through habituation (Grunst et al. 2019b). Contamination could inhibit such effects, limiting exploitation of disturbed habitats. Furthermore, cognition plays a key role in facilitating behavioral adjustment to variable and novel environments, for instance in urban areas (Sol et al. 2005). Thus, cognitive deficits caused by contamination might inhibit behavioral adjustments to environmental change across multiple behavioral domains. In addition, contamination could inhibit plasticity in neural networks that facilitate adjustment of cognitive capacity to environmental conditions. For instance, moderate elevation of CORT improves spatial memory in food caching mountain

chickadees (*Poecile gambeli*) (Pravosudov 2003). Contaminated individuals could fail to display such plasticity due to disrupted HPA axes (Franceschini et al. 2008).

5.5. Juvenile behavior: Juveniles have limited detoxification capacities and are susceptible to organizational effects of contaminants on neural and endocrine systems (Burger and Gochfeld 2005; Ottinger and Dean 2022), which might be exacerbated by multiple stressor exposure, leading to synergistic effects (Lunny et al. 2020). Contaminant exposure could also inhibit behavioral or developmental plasticity that allows juvenile birds to cope with environmental challenges. For example, nestlings fed insufficiently increase CORT and begging rates to stimulate parental effort (Kitaysky et al. 2003). Endocrine disrupting effects of contaminants on glucocorticoid stress responses and feeding motivation could inhibit such plasticity (Franceschini et al. 2008).

5.6. Antipredator and thermoregulatory behaviors: Contaminant-by-environment interactive effects are also likely to operate within other behavioral domains, which are poorly represented by the avian behavioral ecotoxicological literature (and thus not represented in Fig. 1), but are critical in the context of responses to global environmental change. These domains notably include antipredator and thermoregulatory behaviors. The aforementioned study involving risk-taking by Hg-exposed zebra finches exposed to predation risk can also be seen as involving antipredator behavior. This study suggested that exposure to Hg might accentuate antipredator responses, as Hg-exposed finches prolonged feeding latency under predation risk more than unexposed birds (Kobiela et al. 2015). In this case, antipredator responses exacerbate negative effects of contamination on feeding behavior as predation risk increases, leading to synergistic behavioral and fitness effects. On the other hand, studies in non-avian systems have also reported reductions in antipredator behavior in response to contaminants, with individuals failing to reduce activity under risk. To give one example, gray treefrog tadpoles (*Hyla versicolor*) exposed to the pesticide carbaryl failed to increase refuge use under predation risk (Bridges

1999). In this case, antipredator responses are inhibited, leading to antagonistic effects on behavioral change, but the potential for synergistic fitness effects mediated by elevated depredation.

One study involving foraging behavior also reported on thermoregulatory behavior. Great egrets highly exposed to Hg spent more time inactive and in the shade than less exposed birds, in concert with reduced feeding rates (Bouton et al. 1999). These results suggest that rising temperatures could exacerbate negative effects of contamination on foraging behavior, if contaminated birds have impaired thermoregulatory capacity and are thus forced to alter behavior to avoid heat stress (Bouton et al. 1999). In contrast, Pb exposed herring gull chicks failed to learn appropriate behavioral thermoregulation responses (Burger and Gochfeld 2005), suggesting that thermoregulatory responses to rising temperatures could be inhibited by contamination. Inhibition of thermoregulatory responses could entail synergistic effects of temperature stress and contamination on survivorship, which could become increasingly problematic in the context of global warming.

6. Priorities for future research

Our review highlights a deficit of behavioral ecotoxicological studies regarding contaminant-by-environment interactive effects, and the mechanisms underlying these effects. This deficit reflects the challenges of testing complex contaminant-by-environment interactive effects, which requires large sample sizes, and extra investment of time and resources. However, anthropogenic environmental change is exposing organisms to multiple stressors in combination with chemical contamination. Thus, a multiple stressor perspective will be imperative to forming ecologically relevant predictions regarding contaminant-mediated biological effects under global change scenarios. Below we provide guidelines and priorities for designing future studies to fill this research gap, while leveraging our behavioral reaction norm-based conceptual framework for guidance.

Multiple stressor and reaction norm perspectives: A multiple stressor perspective entails recognizing the importance of environmental variability in modifying effects of individual stressors (Crain et al. 2008; Wilson et al. 2021), and our framework posits that multiple stressor, interactive effects on animal

behavior can be better understood from a behavioral reaction norm perspective. Behavioral reaction norms can be accurately quantified only by measuring behavioral patterns across gradients in environmental conditions (e.g. Nocera and Burgess 2002, Esparza et al. 2022). Thus, we encourage laboratory and field researchers to design studies to encompass, rather than control for, variability in multiple co-occurring stressors. For example, laboratory studies should be designed to assess how contamination affects avian predatory behavior across gradients in foraging conditions (e.g. Bouton et al. 1999; Adams and Frederick 2008). Testing for interactive effects and describing reaction norms across environmental gradients requires larger sample sizes than testing for additive effects or executing factorial experiments, especially as interactions may involve more than two stressors (Crain et al. 2008). Consequentially, successfully reaching this research objective will require added expenditure of resources, thought and time by research teams. However, we believe that this extra effort will prove cost effective, as contaminant-by-environment interactive effects may have nontrivial implications for animal behavioral patterns under global change scenarios (e.g. see Esparza et al. 2022; Grunst et al. 2023).

Testing for the range of proposed interactive effects: When applying a reactive norm perspective to test for interactive effects, researchers are encouraged to consider the full range of potential effects highlighted in this review (exacerbation, mitigation, inhibition, convergence). We identified growing evidence for exacerbation effects, wherein behavioral effects of contamination are synergistically increased under stressful conditions, but as of yet very limited evidence for the other pathways. Inhibition entails reduced scope for behavioral adjustment, and could hence be a key mechanism underlying toxicant-induced sensitivity to environmental change (sensu Hooper et al. 2013). Therefore, we particularly encourage studies that explore whether contamination is inhibiting behavioral responses to anthropogenic environmental change across diverse contexts, including changes in resource availability (Amélineau et al. 2019), predation risk (Kubelka et al. 2018), and acoustical environments (Bermúdez-Cuamatzin et al. 2011). Understanding exacerbation, mitigation and convergence effects will also be important to better projecting contamination effects under global change scenarios. For instance, understanding whether antagonistic contaminant-by-environment interactive effects on animal behavior

arise through convergence versus mitigation could be important to predicting management implications. Indeed, mitigation will generally involve amelioration of contamination effects by additional stressors, and is projected to have positive fitness implications. In contrast, convergence involves large declines in performance in less versus more contaminated individuals due to additional stressors, and suggests inability of highly contaminated individuals to capitalize on permissive environmental conditions. Thus, as opposed to mitigation, convergence is not projected to have positive implications for fitness and population stability.

Diverse behavioral domains Researchers are urged to consider the full range of interactive effects across diverse behavioral domains, to broaden perspective on contaminant-by-environment interactions, and implications for responses to environmental change. Most avian behavioral ecotoxicological research has involved reproductive behaviors (see Table S1). In the context of environmental change, more research is particularly needed regarding how contamination and other stressors interact to affect foraging, movement and behavioral performance traits, as plasticity in these traits is central to behavioral adjustments to environmental change. Biologging technologies (accelerometers, GPSs, camera loggers) afford exciting opportunities to link contaminant concentrations to movement and foraging patterns across annual life-history cycles (Fort et al. 2014), and can also grant novel insights into performance traits such as prey capture efficiency in a field setting (Brisson-Curadeau and Elliot 2019).

Mechanistic pathways: Our study highlighted a particular dearth of studies investigating physiological and toxicological pathways underlying contaminant-by-environment interactive effects. To better understand contaminant-by-environment interactive effects on behavior, exploring mechanisms underlying these effects will be critical. Researchers should assess how multiple stressors interact with contaminant exposure to affect endocrine pathways, including the HPA, HPT and HPG axes, and explore parameters related to energy budgets, including metabolic rate, lipid reserves, and daily energy expenditure (DEE). For example, accelerometers can be used to derive time activity budgets and estimate DEE across ranges in environmental conditions (Wilson et al. 2020). Obtaining other physiological measurements, such as oxygen carrying capacity, oxidative status, health status (disease, body condition)

and wing symmetry, will forward understanding of physiological limitations which might constrain performance in highly contaminated individuals (Evers et al. 2008). Field researchers are also encouraged to leverage advances in automated systems designed to test cognition in the field (Morand-Ferron et al. 2015) to investigate cognitive correlates of contaminant exposure, which might limit behavioral plasticity. Finally, understanding how environmental conditions alter the toxicity of diverse classes of contaminants will be important to predicting contaminant-by-environment interactive effects on behavior, as well as other response variables (Hooper et al. 2013).

Identifying sensitive species, populations and individuals Finally, identifying where and when contaminant-by-environment interactive effects are most likely to be manifest and have large downstream effects is an important research priority. Contaminant-by-environment interactive effects on behavior are most likely to strongly impact sensitivity to environmental change in areas where environmental change is progressing rapidly, and contaminant exposure and behavioral performance demands are concurrently increasing. For example, the Arctic is warming >3 times faster than other global regions, melting the cryosphere, reconfiguring trophic networks (IPCC 2021), and increasing behavioral performance demands for many Arctic animals (e.g. Jakubas et al. 2017). Moreover, in some Arctic regions, exposure of marine wildlife to contaminants, such as Hg, is increasing with climate change (AMAP 2021). Thus, understanding contaminant-by-environment interactive effects in the context of climate change is a current research priority of the Arctic Council, and a growing body of Arctic-based research has addressed this topic (e.g. Bustnes et al. 2015; Esparza et al. 2022; Grunst et al. 2023). In comparison to the body of work on Arctic species, little work has addressed contaminant-by-environment interactive effects in tropical regions. However, species inhabiting warm, tropical areas could also be vulnerable to interactive effects of contaminants and environmental stressors on behavioral patterns as global warming progresses, as a tropical species may face more extreme high temperatures. For example, recent work on Australian songbirds has shown limitation of behavior and fitness by heatwaves (Eastwood et al. 2022; Sharpe et al. 2022). Species inhabiting agroecosystems might also be highly vulnerable to contaminant-by-environment interactive effects, as exposure to pesticides and herbicides are elevated in these systems,

often concurrent with reductions in prey species abundance caused by pesticide application (Møller et al. 2021). Researchers should identify species and populations under joint pressure from rising contamination, rapid environment change and intensified behavioral performance demands to guide research effort, and should incorporate a trait-based approach to assess species sensitivity to contaminants and other environmental stressors (Bianchini and Morrissey 2020). In addition, researchers should also consider heterogeneity in sensitivity to contaminant-by-environment interactions on the intraspecific level, as certain life stages (e.g. older individuals that have accumulated toxicants; Burger and Gochfeld 2005), or individuals (e.g. those specialized on feeding at higher trophic levels; Mills et al. 2020) might be especially vulnerable.

7. Conclusions: Our review of the avian behavioral ecotoxicological literature underscores that contaminant-by-environment interactive effects on behavior are understudied, but likely to be prevalent and important, and also highlights a deficit of studies that elucidate mechanisms underlying interactive effects. Specifically, only 17 of 156 (10.9%) avian behavioral toxicological studies have adopted a multiple stressor perspective and investigated contaminant-by-environment interactions, and only 2 of these also considered potential physiological mechanisms. However, 13 of the 17 (76.5%) have found evidence for interactions. We found growing evidence that contaminated individuals might be unable to sustain behavioral patterns upon multiple stressor exposure, leading to steeper behavioral reaction norms and synergistic effects on behavioral change across gradients in additional environmental stressors. In contrast, only a few studies identified in our review suggested antagonistic contaminant-by-environment interactive effects on the magnitude of behavioral change across stressor gradients, which might arise through a number of different avenues, including inhibition of behavioral plasticity. We present a conceptual framework to delineate how contaminant-by-environment interactions might arise via variation in behavioral reaction norm shape, and when synergistic versus antagonistic effects on behavioral change are predicted to arise. We encourage behavioral ecotoxicologists to embrace multiple stressor and behavioral reaction norm perspectives to test for the range of interactive effects proposed,

and better elucidate implications of contamination for animal behavioral responses to global environmental change. More studies are especially needed to elucidate whether contamination inhibits adaptive behavioral responses to stressors associated with global environmental change, as inhibition of such responses could limit population resiliency. Furthermore, we urge ecotoxicologists to incorporate an investigation of physiological, energetic and toxicological mechanisms into behavioral studies, as understanding underlying mechanisms may facilitate mitigation efforts.

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