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1 Combined threats of climate change and contaminant exposure through the lens of bioenergetics

3 Climate change, contamination, bioenergetics

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17 **ABSTRACT** Organisms face energetic challenges of climate change in combination with suites of
18 natural and anthropogenic stressors. In particular, chemical contaminant exposure has neurotoxic,
19 endocrine-disrupting and behavioral effects which may additively or interactively combine with
20 challenges associated with climate change. We used a literature review across animal taxa and
21 contaminant classes, but focused on Arctic endotherms and contaminants important in Arctic ecosystems,
22 to demonstrate potential for interactive effects across five bioenergetic domains: 1) energy supply, 2)
23 energy demand, 3) energy storage, 4) energy allocation tradeoffs, and 5) energy management strategies;
24 and involving four climate change-sensitive environmental stressors: changes in resource availability,
25 temperature, predation risk and parasitism. Identified examples included relatively equal numbers of
26 synergies and antagonies. Synergies are often suggested to be particularly problematic, since they

magnify biological effects. However, we emphasize that antagonistic effects on bioenergetic traits can be equally problematic, since they can reflect dampening of beneficial responses and result in negative synergistic effects on fitness. Our review also highlights that empirical demonstrations remain limited, especially in endotherms. Elucidating the nature of climate change-by-contaminant interactive effects on bioenergetic traits will build towards determining overall outcomes for energy balance and fitness. Progressing to determine critical species, life stages, and target areas in which transformative effects arise will aid in forecasting broad-scale bioenergetic outcomes under global change scenarios.

Keywords: Bioenergetics, energy balance, climate change, chemical contaminants, interactive effects, plasticity, physiological acclimatization, temperature

INTRODUCTION Unprecedented shifts in abiotic and biotic conditions related to climate change pose energetic challenges, including direct effects on metabolism and thermoregulation (Dillon et al. 2010) and indirect effects mediated via trophic dynamics and resource supply (Bartley et al. 2019). Given limited energy budgets, maintaining optimal function under shifting conditions involves differential balance of energetic trade-offs (Norin & Metcalfe 2019). Plasticity may facilitate adaptation (Seebacher et al. 2015), and microevolutionary change may move populations towards new optima (Parmesan 2006; Karell et al. 2011; Norin & Metcalfe 2019). Predicting bioenergetic effects of climate change is a current area of intense research interest (Dillon et al. 2010; Magozzi & Calosi 2015; Clairbaux et al. 2021).

Better forecasting energetic outcomes of climate change depends on recognizing that organisms face climate change-linked challenges in combination with suites of stressors, deeming interactive effects likely. For instance, organisms are exposed to diverse chemical contaminants. Some are transient and exert effects for limited timeframes in proximity to sources (e.g. organophosphate (OP) pesticides; Grue et al. 1982). Others persist in the environment and can reach remote regions through long-range transport (e.g. metals, legacy persistent organic pollutants (POPs; e.g. organochlorine pesticides (OCPs), polychlorinated biphenyls (PCBs)), POPs of emerging concern (e.g. polybrominated diphenyl ethers (PBDEs))) (AMAP 2021a,b). Contaminants have wide-ranging bioenergetic effects, mediated via

neurotoxicity (Calow 1991), detoxification and oxidative costs (Whitney & Cristol 2019), effects on enzymes and mitochondria (Jayasundara 2017) and endocrine disruption (Jenssen 2006; Dietz et al. 2019). Furthermore, energetics traits such as trophic position and movement influence contaminant exposure (Burger & Gochfeld 2004; Michelutti et al. 2010; Lavoie et al. 2012), and are sensitive to environmental conditions.

We evaluated evidence for contaminant-by-climate change interactive effects within five bioenergetic domains: 1) energy supply, 2) energy demand, 3) energy storage, 4) energy allocation tradeoffs, and 5) energy management strategies (EMSs). EMSs describe adjustment of basal metabolic rate (BMR) to conserve energy or support activity, and patterns of covariation between BMR, auxiliary energy expenditure (AEE) and daily energy expenditure (DEE) (Halsey et al. 2019). Figure 1 depicts how non-parallel reaction norms in bioenergetic traits could generate interactive effects between contaminant exposure and climate change-associated environmental stressors.

We reviewed the literature to assess evidence for interactive effects involving four climate change-sensitive environmental variables: resource availability, temperature, predation risk, and exposure and susceptibility to parasitism. Although other shifts in environmental conditions are relevant (e.g. ocean acidification, drought), the abiotic and biotic environmental factors that we focus on are likely to exert effects across ecosystem types. We reviewed evidence for interactive effects on multiple traits within domains 1-3 (Supplementary Material; Table S1 for details), and classified interactive effects via the framework explained in Figure 2 (Supplementary Material for details). For domains 4 and 5 our discussion remains more hypothetical, and focuses on generating testable hypotheses.

We were interested in understanding contaminant-by-environment interactive effects on Arctic endotherms. Climate change is likely to disrupt bioenergetics in Arctic ecosystems, due to rapid warming (IPCC 2021), extensive trophic reorganization (Frainer et al. 2017), organismal adaptations to cope with cold stress (Oswald & Arnold 2012; Gilg et al. 2012), and alterations in biochemical cycling that modify contaminant concentrations in biota (Borgå et al. 2022). For instance, melting permafrost, and increased precipitation and terrestrial runoff may elevate exposure to POPs in aquatic ecosystems (Borgå et al.

2022). Although isolated from contamination sources, the Arctic acts as a sink for volatile contaminants, which persist in cold environments and increase in concentration at higher trophic positions through biomagnification (AMAP 2021a,b). Although levels of legacy POPs (e.g. PCBs) show decreasing trends in the Arctic, these trends are slowing or leveling off, and other POPs (e.g. PBDEs) are often increasing, as are chemicals of emerging Arctic concern (CEAC; e.g. per- and polyfluoroalkyl substances (PFASs); flame retardants). Another important contaminant in the Arctic, mercury (Hg), displays decreasing atmospheric trends, but both increasing and decreasing trends have been observed in biota (AMAP 2021a). Thus, cumulative contaminant impacts are likely to increase in the Arctic in coming decades (AMAP 2021b). We used the Arctic Monitoring and Assessment Programme report, listing contaminants of concern in the Arctic (AMAP 2021), to guide our literature search (Supplementary Material for details). Given the few studies assessing interactive effects on Arctic organisms (Table 1), we expanded our review to encompass all animal taxa, while frequently incorporating discussions of how interactive effects might affect Arctic endotherms.

INTERACTIVE EFFECTS ACROSS BIOENERGETIC DOMAINS

Table 1 summarizes studies on contaminant-by-environment interactive effects across bioenergetic domains. This table highlights a deficit of research involving endotherms in general, and Arctic endotherms in particular, and a bias towards testing interactive effects with temperature and metals. Results suggest relative balance between synergistic and antagonistic effects and more unpredictable interactions than simple additive or non-significant effects. However, our emphasis was not on comparing the frequency of interactive effects, as we did not formally calculate effect sizes. Below, we discuss interactive effects within each bioenergetic domain and underlying mechanisms.

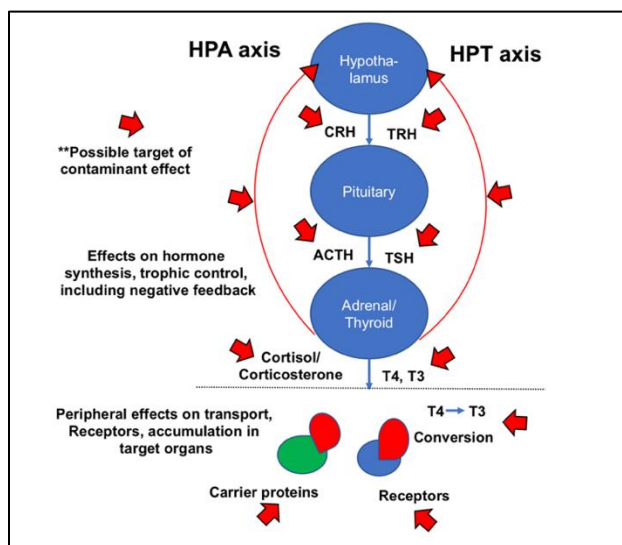
Energy supply

Foraging and ingestion

Contaminant-by-temperature interactive effects on foraging. Empirical demonstrations of contaminant-by-temperature interactive effects on foraging remain limited, with only 6 studies, and none on

endotherms (Table 1, S2). However, many contaminants interfere with the thyroid hormone system, which is central to thermoregulation (Box 1), and high temperatures may increase chemical toxicity (Hooper et al. 2013). Thus, contaminant exposure could amplify the need to forage in reduced spatial ranges or temporal windows given thermal challenge (Rabaiotti & Woodroffe 2019), resulting in negative synergy and magnifying effects on energy intake. Indeed, Hg exposure was associated with more time spent inactive in the shade in great egrets (*Ardea alba*) (Bouton et al. 1999). Combined effects of thermal stress and contamination might be especially pronounced in species occupying niches close to the upper critical limit of thermal neutrality, in regions that are warming rapidly (e.g. the Arctic; AMAP 2021), and in high latitude or elevation species poorly adapted to dissipate heat (Blix 2016).

Box 1. Endocrine pathways through which contaminants may disrupt metabolism: Contaminants can interfere with physiological mechanisms, including the hypothalamus-pituitary-adrenal (HPA) and hypothalamus-pituitary-thyroidal (HPT) axes, which mediate adjustment of metabolism to conditions.



Steroid glucocorticoids (GCs) released via the HPA axis support glucose metabolism, mediate vertebrate stress responses (Sapolsky et al. 2000; McEwen & Wingfield 2003), and aid in temperature-dependent regulation of metabolic rate (MR) (Jimeno et al. 2018). Corticotropin releasing hormone (CRH) is involved in primary thermogenesis through its effect on

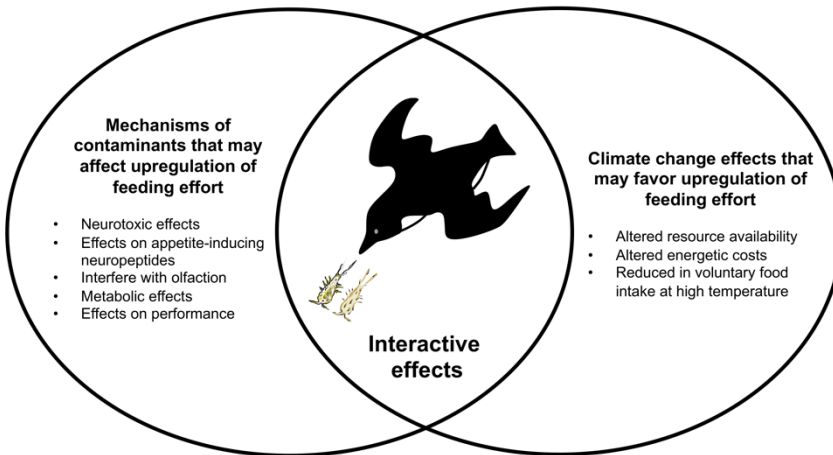
thyroid stimulating hormone (TSH) (De Groef et al. 2006). The HPT axis mediates oxygen consumption, ATP use, and thermogenesis through release of THs, thyroxine (T_4), and 3,5,3-triiodothyronine (T_3) (Yen 2001; Leemans et al. 2019; Ruuskanen et al. 2021).

Contaminants affect hormonal axes via diverse mechanisms, including interference with receptors, carrier proteins, hormone release or negative feedback. Metal- and POP-exposure can both elevate GCs

and suppress HPA sensitivity (Tartu et al. 2014; Monclús et al. 2018). OC- and PCB-exposure may decrease THs via direct action on the thyroid, interfering with transport proteins, or disrupting deiodinases, such as those converting T_4 to T_3 (Wada et al. 2009; Leemans et al. 2019). Conversely, PFASs have been positively associated with THs (Melnés et al. 2017; Ask et al. 2021). In black-legged kittiwakes (*Rissa tridactyla*), PFASs positively correlated with T_4 in males and T_3 in females, with the mechanism involving competition with THs for binding proteins (e.g. albumin). Increased THs could elevate BMR, interfere with thermal acclimation and reduce tolerance to cold or heat (Ask et al. 2021).

Contaminant-by-resource availability interactive effects on foraging. In endotherms, six studies tested for contaminant-by-resource availability interactive effects on foraging behavior (Table 1, S2). This dearth of research is regrettable, given extensive potential for these effects. Climate change is affecting resource availability and distribution, causing shifts in trophic dynamics (Parmesan 2006; Lurgi et al. 2012). For example, in the Arctic, climate change is reducing availability of sea ice-associated prey, such as lipid-rich copepods and fish (e.g. Arctic cod; *Boreogadus saida*) utilized by seabirds (Gaston et al. 2009; Divoky et al. 2015; Amélineau et al. 2019), and seals preyed on by polar bears (*Ursus maritimus*) (Stirling & Derocher 2012). Evolving precipitation and wind regimes also pose challenges. For example, as wind speed increases, flight costs increase and seabirds may deliver less energy to nestlings (Elliott et al. 2014), and freezing rain in the Arctic elevates energetic costs for terrestrial animals seeking plants or small rodents (Gilg et al. 2012). Given decreased resource availability or quality, organisms may increase foraging effort and DEE to stabilize energy intake (Welcker et al. 2009), or decrease activity and energy intake to conserve energy (Stirling & Derocher 2012). Box 2 discusses mechanisms by which contaminant exposure might disrupt such responses, potentiating interactive effects.

Box 2. Mechanisms of contaminant-linked effects on upregulation of foraging effort: Neurotoxic effects can compromise locomotion, reducing foraging efficiency (Kobiela et al. 2015; Ecke et al. 2017). Contaminant exposure can also affect foraging motivation through actions on appetite-inducing or suppressing neuropeptides, and interfere with olfactory detection of prey (Groh et al. 2015). In



endotherms, reduced appetite and voluntary food intake at high temperatures, which adaptively reduces digestion-related heat production, could magnify these effects (Youngentob et al. 2021).

Contaminants may also influence foraging effort by affecting metabolic parameters. For example, Hg can reduce metabolic scope (Clarke & Pörtner 2010) and impair performance by suppressing hemoglobin production and oxygen carrying capacity, and binding with thiol-containing enzymes and carrier proteins (Olsen and Evers 2000; Gerson et al. 2019a; Seewagen 2020). Contaminants' effects on metabolism and foraging could additionally be mediated through body condition. Arctic belugas (*Delphinapterus leucas*) in poor condition had lower oxygen stores, which may affect diving depth and aerobic dive limits (Choy et al., 2019). Finally, effects on cognition such as reduced spatial memory, inability to assimilate information, or compromised neurological processes could increase search costs (Swaddle et al. 2017; Saaristo et al. 2018).

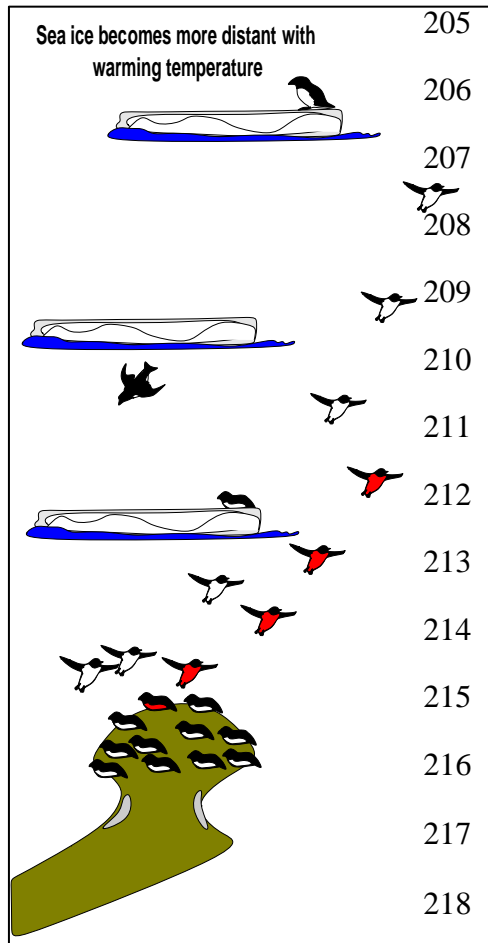
Examples of contaminant-by-resource availability interactive effects in endotherms include a study on Arctic thick-billed murres (*Uria lomvia*) exposed to Hg, which displayed altered T_3 only during years with suboptimal conditions associated with advanced sea ice breakup. Elevated T_3 was associated with reduced diving, which could result in negative synergistic effects on energy intake (Esparza et al. 2022).

As T_3 is positively associated with MR in murres (Elliott & Gaston 2014), this effect could reflect a tradeoff between increased oxygen consumption and energy-intensive behavior.

Contamination may dampen increases in foraging effort, undermining ability to maintain energy intake given resource shortage, or increase intake to exploit abundant resources, resulting in positive antagonism. For example, Arctic organisms contaminated by pollutants such as Hg, a contaminant of concern in the Arctic, may be unable to employ energetically-intensive behaviors required to track spatial changes in resources associated with the cryosphere (Meredith et al. 2019; Box 3). Contamination could also dampen functional responses that enable organisms to capitalize on transient resource peaks, such as algae blooms triggered by melting sea ice (Eamer et al. 2013; Meredith 2019). Although evidence from the Arctic remains lacking, Hg contamination dampened predator functional responses of great egret (*Ardea albus*) to increased prey detectability (Bouton et al. 1999).

Contamination could also affect animals' ability to phenologically track shifting resource peaks, for instance by deeming individuals unable to advance breeding under warmer conditions (Charmantier et al. 2008). Evidence exists of contaminated birds delaying egg laying date (Helberg et al. 2005; Bustnes et al. 2007), but interactive effects with environmental conditions remain largely unexplored. One study reported a non-intuitive result. Common eiders (*Somateria mollissima*) laid later in warmer years, with this effect less pronounced in Hg-exposed females (Smith et al. 2022). The mechanism underlying this effect was postulated to involve disruption of the HPA axis by Hg (Smith et al. 2022).

Furthermore, contaminants could limit downregulation of foraging in response to resource shortage, which can conserve energy (Cuyler & Øritsland 2011; Stirling & Derocher 2012). In Arctic animals, such as the Arctic fox (*Vulpes lagopus*), decreased activity and MR serve as adaptations to winter food scarcity (Prestrud 1991). Sustained foraging effort despite resource shortage could result in a negative antagonistic effect on foraging activity, but a negative synergistic effect on energy balance. Such an effect remains undocumented, but could arise due to stimulatory effects of some contaminants. For instance, Hg-exposed golden shiners (*Notemigonus crysoleucas*) displayed hyperactivity, increasing energy expenditure (Webber & Haines 2003).



Box 3: Hypothetical inhibition of foraging plasticity by Hg

exposure: Little auks (*Alle alle*) depend on sea ice-associated copepods, which are being replaced by less lipid-rich species due to climate change-linked sea ice declines. Birds can travel farther and use novel foraging areas along melting glaciers to stabilize energy intake (Jakubas et al. 2013; Grémillet et al. 2015). However, Hg in copepods in Greenland have been increasing with climate change, driving increases in Hg in little auks (Fort et al. 2016). Neurotoxic effects of Hg may dampen reaction norms, resulting in a positive antagonistic interaction between warming and Hg contamination on foraging behavior. In particular, increasing flying and diving, which have energetic costs of ~ 7.24 and $9.37 \times \text{BMR}$ (Ste-Marie et al. 2022), could prove untenable for contaminated birds (in red) with reduced

metabolic or locomotory efficiency, forcing reliance on lower quality resources and jeopardizing fitness (Amélineau et al. 2019).

Finally, climate change-associated declines in resource availability or quality could elevate contaminant exposure and/or toxicological effects, inducing interactive effects. Contaminant concentrations often rise with declines in body mass and adipose or muscle tissue (Bustnes et al. 2010; Peterson et al. 2018). In northern elephant seals (*Mirounga angustirostris*), blood Hg increased by 103% during the breeding season fast in association with increased blood volume and muscle tissue (Peterson et al. 2018), and lipophilic PCBs were mobilized from blubber to blood during the post-weaning fast (Debier et al. 2006). Furthermore, climate change-induced fluctuations in prey availability could force predators to exploit alternative prey, influencing contaminant loads. With warming conditions, Greenlandic polar bears shift to exploit subarctic hooded (*Cystophora cristata*) and harp seals (*Phoca*

groenlandica), which have higher POP loads than arctic ringed seals (*Pusa hispida*). This diet shift is dampening declining trends (linked to decreased emissions) in the POP loads of polar bear adipose tissue (McKinney et al. 2013). Altered resource dispersion and search costs associated with climate change could also affect food intake rates, creating feedbacks. For instance, in canvasback ducks (*Aythya valisineria*) Cd uptake declines with increased resource dispersion, which increases search costs and decreases food intake (Lovvorn & Gillingham 1996).

Contaminant-by-predation risk interactive effects on foraging. Evidence also exists for contaminant-by-predation pressure interactive effects on foraging behavior, although only one study focused on endotherms (Table 1, S2). Heightened risk-sensitivity in Hg-exposed zebra finch induced larger reductions in foraging under predation risk, leading to a negative synergistic effect on energy intake (Kobiela et al. 2015). Alternatively, as suggested for zinc (Zn)-exposed damselfly larvae (*Ischnura elegans*), contaminated individuals with heightened energetic costs might be unable to tradeoff foraging against vigilance, canalizing reaction norms and generating negative antagonism (Janssens et al. 2014). A similar outcome is predicted if contaminants interfere with predator cue detection (Ehram et al. 2016). Conversely, positive antagonism might arise if energetically-stressed contaminated individuals increase foraging effort only in absence of predation risk, as in Cd-exposed mayfly nymphs (*Baetis tricaudatus*) (Riddell et al. 2005). Importantly, climate change can either intensify or ameliorate predation risk. For instance, sea ice loss reduces predation on ground-nesting seabirds by denying Arctic foxes access to island colonies (Chaulk et al. 2007; Eamer et al. 2013), but increases predation from polar bears, which shift from marine to terrestrial resources earlier in the season (Iverson et al. 2014). Actions of contaminants on risk sensitivity, or ability to balance tradeoffs, may mediate Arctic animals' responses to shifting predation pressures, but empirical examples remain lacking.

Assimilation and metabolic efficiency

Studies documenting contaminant-by-environment interactive effects on assimilation (AE) and metabolic (ME) efficiency were exclusively on ectotherms, and primarily involved interactions with temperature

(Table 1, S3). Many contaminants affect parameters important to AE and ME. For example, metal exposure can cause anemia, compromise oxygen transport by hemoglobin (Calisi et al. 2011), interfere with enzymes involved in glycolysis and electron transport, and increase mitochondrial protein leak, reducing ATP production (Sokolova & Lannig 2008; Branca et al. 2020). Exacerbation of effects at high temperature may be mediated by increasing toxicity, generating negative synergy. For example, high temperatures induced stronger, rapider Cd-related declines in digestive enzyme function in threespine stickleback (*Gasterosteus aculeatus*) (Hani et al. 2018). Examples of negative antagonistic interactions also exist. For instance, a flame retardant's negative effect on AE in white seabream (*Diplodus sargus*) declined at higher temperatures, perhaps reflecting enhanced contaminant metabolism and clearance at higher temperature, or higher growth rates (Anacleto et al. 2018).

A few studies explored interactive effects of contaminants with predation risk and parasitism. One reported a significant interaction (Table 1, S3), wherein two POP pesticides, atrazine and endosulfan, combined with predation risk to have a negative synergistic and negative antagonistic effect, respectively, on the AE of damselfly larvae (*Coenagrion puella*) (Campero et al. 2007). Resource availability could also interact with contamination to affect AE and ME, although no empirical demonstrations exist. Climate-change related shifts in prey use or availability may reduce AE, exacerbating contaminant effects and reduce trophic energy transfer. Thick-billed murrelets displayed 5.6% higher AE when fed on cold-associated Arctic cod than on capelin (*Mallotus villosus*), a difference explained by cod's higher fat content. This relationship could be modified by contaminant exposure if effects of contaminants on enzyme function depend on food nutrient content (Brekke & Gabrielsen 1994).

Energy demand

Metabolism

Contaminant-by-temperature interactive effects on metabolism. Examples of contaminant-by-environment interactive effects on metabolic traits primarily involved metabolic responses of individuals to temperature challenge (Table 1, S4). In endotherms, cold-associated increases in BMR are driven by

increasing sizes of organs involved in energy acquisition and assimilation, which enhances body temperature maintenance and survival, while decreased BMR at warmer temperatures conserves energy and limits need for heat dissipation (McKechnie 2008). Contaminant exposure could interfere with the ability to adjust MR to temperature, generating interactive effects. For example, mice exposed to arsenic (As) displayed reduced oxygen consumption and energy expenditure only when thermally challenged. This positive antagonistic effect could compromise thermoregulatory capacity, compromising survivorship (Castriota et al. 2020). Such an effect could reflect endocrine disruption by contaminants, which can increase or suppress MR. For example, in Arctic breeding black-legged kittiwakes, BMR correlated positively with perfluorotridecanoate (a PFAS) levels in females, but negatively with the sum of detected chlordanes (an OC metabolite) in both sexes (Blévin et al. 2017). Opposing effects of these contaminant types may reflect different actions on the HPT axis (Box 1). Furthermore, contaminants, such as methylmercury, can limit mitochondrial oxidation and ATP production, which could suppress MR, limiting capacity for upregulation (Gonzalez et al. 2005).

Other contaminant-by-environment interactive effects on metabolism. Animals often adjust MR in response to resource levels, and contaminant exposure may interfere with these responses, as indicated by some research, limited to ectotherms (Table S4). For example, lake chubsuckers (*Erimyzon sucetta*) exposed to metals reduced standard metabolic rate (SMR) less when subjected to food limitation than unexposed fish, resulting in negative antagonism (Hopkins et al. 2002). SMR could be elevated by detoxification costs (Verreault et al. 2007), limiting downregulation and interfering with an important energy conservation mechanism. In contrast, food limitation magnified suppressive effects of PCBs on lipid metabolism in Arctic char (*Salvelinus alpinus*), resulting in a negative synergistic effect that could compromise energy balance (Vijayan et al. 2006).

Changes in predation risk linked to climate change could also induce changes in metabolism that are sensitive to contaminant exposure, with possible responses including acute increases to support fight-flight responses, or decreases reflecting suppressed activity and increased refuge use (Tan et al. 2020).

However, neither of two studies examining contaminant-by-predation risk effects on metabolism reported significant interactions (Burraco et al. 2013; Tan et al. 2020).

Finally, in the only study testing contaminant-by-parasitism interactive effects on metabolism, parasitism elevated activity of the electron transport system in Cockle (*Cerastoderma edule*), but arsenic (As) exposure reduced this effect (Magalhães et al. 2018). This positive antagonistic effect could limit the ability to elevate energy expenditure to combat infection.

Thermoregulation

Contaminant-by-temperature interactive effects on thermoregulation. Empirical demonstrations of contaminant-by-temperature interactive effects on thermoregulation in endotherms are limited to four studies (Table 1, S5). For example, Hg contamination and high temperature synergistically reduced tree swallow (*Tachycineta bicolor*) nestlings' survival, which was hypothesized to reflect impaired thermoregulatory capacity via disrupted THs (Hallinger & Cristol 2011; Table S4). In ectotherms, considerably more work has been done (Table 1, S5). For instance, exposure to copper (Cu) and the legacy POP dichlorodiphenyltrichloroethane (DDT) narrowed the thermal tolerance window in medaka fish (*Oryzias melastigma*), and exposure to high temperatures and the contaminants synergistically decreased heat shock defense mechanisms (Li et al. 2022). In addition, carabid beetles (*Platynus assimilis*) exposed to an insecticide were unable to maintain body temperature and survive as temperature increased (Merivee et al. 2015).

Although largely undocumented, contaminant-by-temperature interactive effects on thermoregulation may be important in Arctic endotherms, due to their unique thermal biology. Arctic animals have adaptations, such as subcutaneous fat and short legs, that minimize heat loss, increasing risk of heat stress (Blix et al. 2016; O'Connor et al. 2021). For example, due to subcutaneous fat stores, Arctic reindeer (*Rangifer tarandus*) rapidly generate excess heat when exercising, and have evolved specialized blood flow patterns to prevent cerebral overheating (Blix et al. 2016). High latitude animals from cold climates

also often have lower surface area to volume ratios to conserve heat (Scholander et al. 1950), and higher MRs than other species of comparable body size, amplifying risk of heat stress (Choy et al. 2021).

Mechanistically, contaminant-by-temperature interactive effects on thermoregulation may reflect disrupted acclimatization responses. For instance, small birds overwintering in temperate zones employ facultative hypothermia to conserve energy (McKechnie & Lovegrove 2002), and increase cold tolerance by elevating BMR and reducing thermal conductance (Douglas et al. 2017). Endotherms also display facultative hyperthermia to reduce need for water to drive evaporative cooling (Hetem et al. 2014; Douglas et al. 2017; Gerson et al. 2019b). On a related vein, endotherms can adjust heat dissipation capacity to maintain optimal function (Speakman 2018). In lieu of effective heat dissipation, hyperthermia results, which can damage proteins, induce oxidative stress or be fatal (Speakman & Król 2010; Tapper et al. 2020; Rogers et al. 2021). Heat dissipation capacity has strong effects during energy-intensive life-history stages, such as lactation (Speakman & Król 2010; Zhao et al. 2020), or nestling provisioning (Tapper et al. 2020), and may limit DEE in Arctic animals adapted to retain heat (Blix 2016), and large animals with low surface area to volume ratios (Rogers et al. 2021). Box 4 discusses physiological mechanisms that could underlie disruption of thermoregulatory responses by contaminants, generating interactive effects.

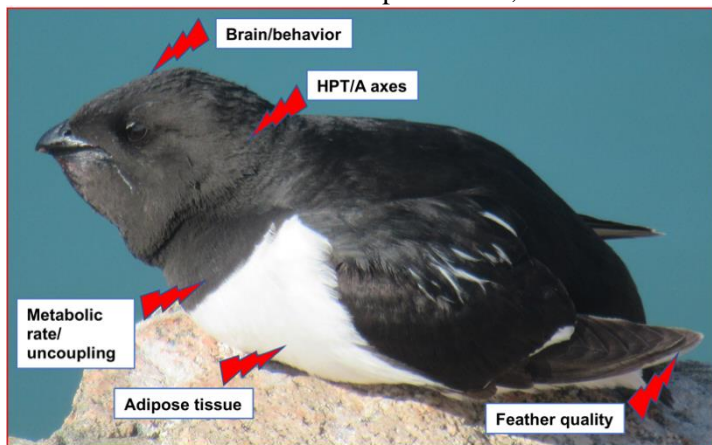
Projected gradual increases in mean temperatures are within the range of acclimatization responses, and may not result in thermal stress (McKechnie 2008), especially at high latitudes (Fort et al. 2009; Amélineau et al. 2019). However, adjustments in BMR and body temperature can occur between and within days (McKechnie 2008). Thus, climate change-linked increases in temperature fluctuations and extreme weather (Meehl & Tebaldi 2010) could increase potential for contaminant-linked changes in BMR and thermal setpoints to compromise energy balance. Furthermore, at higher temperatures, increasing detoxification costs, bioavailability and toxicity, and cellular damage related to heat stress could cause synergistic increases in BMR and thermal challenge (Verreault et al. 2007; Hooper et al. 2013). Conversely, warmer temperatures sometimes increase contaminant clearance (Noyes et al. 2009), which might ameliorate detoxification costs, reduce BMR, and generate antagonistic effects.

Other types of contaminant-by-environment interactive effects on thermoregulation. Contaminant exposure might also interact with environmental variables besides temperature to affect thermoregulation (Table 1, S5). For example, a positive synergistic interaction occurred between radioactivity exposure and nutritional stress in barn swallows (*Hirundo rustica*) (Boratyński et al. 2021). Birds in poor condition upregulated body temperature more with radioactivity exposure, compromising energy balance and increasing risk of overheating. Similarly, in damselfly larvae (*Ischnura elegans*), exposure to an organophosphate (OP; chlorpyrifos), a CEAC, reduced heat tolerance, but only when competition for resources was high (Op de Beeck et al. 2018). Predation risk and parasitism could also combine with contamination to affect thermoregulatory ability via effects on behavior and energy balance. However, the two studies testing for such effects reported additive results (Table 1, S5).

Contaminant-by-environment interactive effects on behavioral thermoregulation. A limited number of studies on ectotherms have reported contaminant-by-environment interactive effects on behavioral thermoregulation (Table S5). Neurotoxic or endocrine disrupting effects of contaminants can interfere with behavioral plasticity that facilitates thermoregulation, such as foraging during crepuscular periods to avoid thermal stress (Hetem et al. 2014). In addition, behavioral thermoregulation strategies often entail tradeoffs, with which contaminated individuals might be unable to cope. For instance, microhabitats selected for thermoregulatory advantages may have lower food availability or increased predation risk (Hetem et al. 2014). Furthermore, the behavioral thermoregulatory strategy that proves adaptive may be altered when temperature and contaminant stress are experienced in combination, relative to in single stress scenarios. For example, Mongolia racerunners (*Eremias argus*) exposed to the insecticide abamectin displayed higher body temperature preference as a detoxification mechanism. However, lizards jointly exposed to abamectin and heat stress simultaneously face elevated MR and repair costs linked to contaminant and heat exposure, and decreased locomotion and predatory performance caused by contamination. Under this extreme stress, lizards shift to display a heat-avoidance reaction, resulting in a positive synergistic effect on thermal shelter use, which is a short-term means of conserving energy, but might ultimately compromise energy balance (Nie et al. 2022).

Box 4: Mechanisms through which contaminants could interfere with thermoregulation:

Contaminant exposure may interfere with thermoregulation via endocrine disruption, with effects on the HPT axis particularly relevant, due to its role in mediating thermoregulation in vertebrates (Verreault et al. 2004, 2007; Wada et al. 2009). Contaminants could also impact thermoregulation via effects on body composition (more lean versus adipose tissue) and the integument (feather, fur quality). Contaminated individuals often have less adipose tissue, which increases heat loss and decreases metabolic capacity



(Eckbo et al. 2019). Conversely, contaminants associated with lipid accumulation (“obesogens”; Grün & Blumberg 2009) may interfere with upregulation of heat dissipation as temperatures increase, generating an antagonistic effect on body temperature and

limiting DEE. Poor quality feathers or fur could also increase thermal conductance, increasing need to elevate MR to maintain body temperature. In addition, contamination could interfere with microvasodilation or constriction responses that affect cutaneous evaporation, impair behavioral responses such as panting and gular flutter, modify activity patterns (McKechnie & Wolf 2019), and alter mitochondrial function via uncoupling protein (UCP) (Demine et al. 2019). In mammals, UCPs control dissipation of the proton gradient across the mitochondrial membrane, enhancing thermogenesis. T_3 also regulates uncoupling, further implicating the HPT axis as a target of contaminant-mediated effects on thermoregulation (Demine et al. 2019). Finally, contaminants can elicit changes in homeostatic temperature regulation, which could interfere with responses to environmental conditions. For instance, hypothermia often occurs in rodents exposed to contaminants, and heat stress may exacerbate toxicity by overriding this response (Gordon et al. 1990; Leon 2008; Holmstrup et al. 2010).

Physical activity

DEE correlates with physical activity in free-living animals and can predict fitness (Grémillet et al. 2018; Wilson et al. 2020), suggesting importance of contaminant-by-environment interactive effects on activity. Table S1 gives relevant examples for foraging activity. Examples pertaining to activity in other contexts mostly involved interactive effects of contaminant exposure with predation risk or temperature, and all but two were on ectotherms (Table 1, S6).

Contaminant-by-temperature interactive effects on activity. Eleven studies (one on endotherms) reported significant contaminant-by-temperature interactive effects on activity, with no one interaction type clearly dominating. For instance, female mice (*Mus musculus*) prenatally exposed to methylmercury showed inactivity during an open field test, but this effect was dampened in combination with thermal stress, resulting in negative antagonism (Yin et al. 1997). Different types of contaminant-by-temperature interactive effects on activity are predicted to have distinct implications for energy balance. For example, rising temperatures can elevate activity-related energy costs in endotherms. Heat generated by activity offsets thermoregulatory costs under cold conditions (Careau & Garland 2012), but must be dissipated as temperature rises, via vasodilation and evaporative water loss (McKechnie & Wolf 2019; O'Connor et al. 2021). Thus, thermally-stressed organisms may downregulate activity to conserve energy and water, a strategy that may be disrupted by negative antagonistic or positive synergistic interactive effects with contaminants. Conversely, increasing temperature may increase performance, especially in ectotherms, and this effect may be dampened via positive antagonistic interactions with contamination (e.g. Quiroga et al. 2019).

Contaminant-by-predation risk interactive effects on activity. Seven studies on ectotherms (no studies exist on endotherms) reported negative antagonistic interactions between contaminant exposure and predation risk (Table 1, S6). For example, metal-exposed round goby (*Neogobius melanostomus*) downregulated activity less than unexposed individuals under predation risk (Marentette & Balshine 2012). A similar effect could be classified as positive synergy, if activity in contaminated individuals under predation risk is greater than the additive prediction (e.g. Preston et al. 1998; Janssens & Stoks

2012). As for foraging, this interactive effect could reflect neurological effects of contaminants that promote hyperactivity, or need to maintain high energy intake to cover detoxification costs. Sustained activity under predation risk could have fitness implications. For example, in the rotifer (*Brachionus calyciflorus*), pentachlorophenol exposure reverses adaptive decreases in swimming speed that reduce predator encounters rate, with exposed *B. calyciflorus* displaying an ~30% increase in swimming speed in presence of the predatory rotifer (*Asplanchna girodi*), elevating predation risk by ~50% (Preston et al. 1998). In contrast, a negative synergistic effect between predation risk and contaminant exposure was observed in wolf spiders (*Pardosa milvina*), which only reduced movement in response to cues from predatory carabid beetles (*Scarites quadriceps*) if exposed to a glyphosate-based herbicide (Wrinn et al. 2012).

Immune defense

The immune system is a complex, costly component of energy demand (Sheldon & Verhulst 1996) which is vulnerable to contaminant-by-environment interactive effects. Of four studies testing for such effects in endotherms (Table 1, S7), one reported a possible interaction, involving one of three metals studied. More specifically, parasitism moderately reduced Hg-induced elevation of superoxide production by macrophages in mouse (*Mus musculus*) (Jalčová & Dvorožnáková 2014). Such positive antagonistic effects between parasitism and contaminant exposure could reflect sequestering of contaminants by the parasite. Stimulatory and suppressive effects of contaminants on immune parameters in endotherms have been reported (Desforges et al. 2016; Vallverdú-Coll et al. 2019), with diverse mechanisms implicated, including interference with the aryl hydrocarbon receptor (Suzuki et al. 2020; Bou Zerdan et al. 2021). For instance, in polar bears, PCBs and OCPs have immunosuppressive effects on circulating immunoglobulin class G, production of viral antibodies, and proliferation of T and B lymphocytes (Routti et al. 2019). These impairments might heighten sensitivity to intensified pathogen regimes (Sonne 2010; Desforges et al. 2016; Dietz et al. 2019). For Arctic endotherms, contaminant-by-environment interactive effects on the immune system may pose a poignant threat, since the Arctic is characterized by low

pathogen levels, deeming organisms maladapted to cope with increases in pathogen prevalence under climate change (Bradley et al. 2005; Sonne 2010; Routti et al. 2019).

In ectotherms, studies have reported both synergistic and antagonistic interactions between contaminant exposure and other environmental stressors (Table 1, S7). For example, in black sea bream (*Acanthopagrus schlegelii*) positive effects of Zn on phagocytosis and lysosome activity were increased at higher temperature, which could prime organisms to cope with pathogen challenge, but magnify effects on energy demand (Kim et al. 2017). On the other hand, in Pond snails (*Physa gyrina*), a stimulatory effect of the herbicide atrazine on hemocyte numbers disappeared under predation pressure (Sandland & Carmosini 2009). This positive antagonistic interaction could reflect reduced energy intake under predation risk, deeming increased energy investment in response to contaminant exposure impossible or unbeneficial.

Energy storage

The balance between energy supply and demand affects energy storage capacity, which is critical during particular life history stages, such as prior to migration or hibernation (Guglielmo 2018; Weitten et al. 2018), before breeding in capital breeders (Gauthier et al. 2003), and in animals preparing for winter resource scarcity (Blix 2016). Since certain diets promote or hinder fatty acid synthesis (Weitten et al. 2018), climate change-related shifts in resource availability may be detrimental to energy storage. Scarcity of essential food resources during critical periods may force animals to use alternative resources, or increase spatiotemporal scope of foraging effort. Contaminant exposure may combine with climate change-related effects on energy storage through a variety of mechanisms (Box 5).

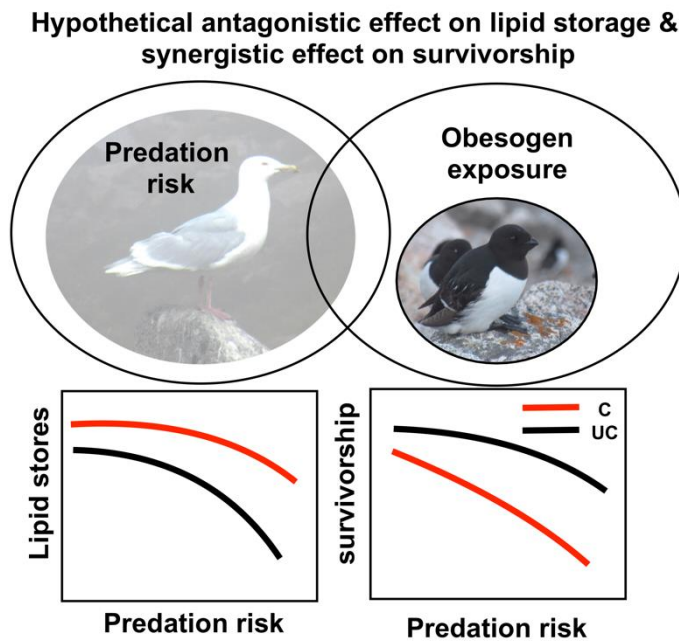
Two studies tested for contaminant-by-environment interactive effects on variables related to energy storage in endotherms, both involving metal contamination in birds (Table 1, S8). First, there was no interactive effect between metal contamination and weather conditions, including temperature, on body condition of tree swallows (Beck et al. 2015). Second, Hg-exposed zebra finches lost more mass than controls only under predation risk, resulting in a negative synergistic interaction that was mediated by

increased risk sensitivity (Kobiela et al. 2015). Given climate change-linked elevation in predation risk, such an effect could further undermine contaminated organisms' ability to store energy.

In ectotherms, studies reporting contaminant-by-environment interactive effects on energy storage all involved temperature (Table 1, S8). In Cope's gray tree frog (*Hyla chrysoscelis*), metal exposure and elevated temperatures synergistically reduced body condition, reflecting combined effects of elevated MR at high temperatures and detoxification costs (Hallman & Brooks 2016). In contrast, in goldfish (*Carassius auratus*), a negative antagonistic effect occurred in which a POP-containing pesticide mixture decreased the hepatosomatic index (reflecting energy reserves) and muscle protein content at control, but not elevated temperatures (Gandar et al. 2016). Studies in ectotherms also assessed combined effects of contamination and parasitism, predation risk and food shortage, but none reported significant interactions (Table 1; S8).

Box 5. Mechanisms underlying effects of contaminants and climate change on energy storage.

Contaminant exposure may disrupt metabolic processes and behavioral plasticity facilitating energy



storage, and potentially exacerbating climate change-linked stress through cumulative effects that may be additive or interactive. For instance, some flame retardants and PCBs promote lipid accumulation, disrupting body mass regulation (Grün & Blumberg 2009). These obesogens interfere with endocrine regulation of metabolism and neuroendocrine effects on appetite and feeding, and are implicated in metabolic syndromes and obesity

in humans (Grün & Blumberg 2009), and inappropriate weight gain in animals (Martinson & Fernie 2019). Obesogens have potent effects early in life, predisposing individuals to altered metabolic profiles

(Muscogiuri et al. 2017), and in the wild, where decreased maneuverability jeopardizes fitness (Marteinson & Fernie 2019). Altered predation pressure under climate change, such as that of glaucous gulls (*Larus hyperboreus*) on little auks (Wojculanis et al. 2005), could favor decreases in lipid reserves to increase maneuverability. Obesogens could block downregulation of lipid storage under elevated predation risk, resulting in an antagonistic effect on lipid storage (left), but synergistic effect on survivorship (right) (C= contaminated, UC= uncontaminated). Conversely, Cd has disruptive effects on lipid metabolism and storage in fish, mammals and birds (Pierron et al. 2007; Larregle et al. 2008; Lucia et al. 2010), and methylmercury also interferes with lipid metabolism (Moreira et al. 2012). These effects may be magnified by climate change if warmer temperatures increase chemical toxicity, resulting in a synergistic interaction. In addition, contaminant-linked appetite suppression may block increased feeding and accumulation of energy reserves, with this effect magnifying negative effects on energy storage under low resource availability (Groh et al. 2015).

Energy allocation

Assuming limited energy budgets, organisms must tradeoff allocating energy between competing functions, such as survival and reproduction (Van Noordwijk & de Jong 1986). Climate change and contaminant exposure may combine in diverse fashions to interactively affect energy allocation.

Shifting investment towards self-maintenance. First, climate change might intensify energetic tradeoffs between survival and reproduction by shifting environmental conditions away from the optimum, reducing resource availability or quality, leading to mismatches between breeding phenology and resource peaks (Thomas et al. 2001), and increasing energy demands, such as immune costs. In this scenario, organisms may enter an emergency life-history stage, and reduce energy investment into reproduction (Wingfield et al. 1998; McEwen & Wingfield 2003). Contaminant exposure could lower the threshold in environmental challenge (e.g. resource shortage) at which individuals terminate reproduction, by impairing energy reserves and resource garnering capacity, leading to a negative synergistic effect. Contaminant exposure has been associated with reduced incubation attentiveness (Tartu et al. 2015),

offspring provisioning (Evers et al. 2008), and reproductive success (Tartu et al. 2016), although interactive effects with climate change-linked environmental variables remain undocumented.

Contaminant effects on reproductive effort may be linked to effects on hormones that mediate reproductive effort, including CORT, prolactin and luteinizing hormone. For instance, prolactin and Hg levels negatively correlated in two polar seabirds, the black-legged kittiwake and snow petrel (*Pagodroma nivea*), with breeding success in kittiwakes also suppressed (Tartu et al. 2015, 2016). Contaminant-linked disruption of hormones could undermine adjustments in reproductive effort with environmental change. Research suggests synergistic effects of environmental conditions and contamination on reproductive investment and success. For example, south polar skuas (*Catharacta maccormicki*) exposed to mirex (an organochlorine insecticide) and DDT reduced nest defense and displayed increased reproductive failure only in a year of high environmental stress, characterized by high baseline CORT (Goutte et al. 2018). Baseline CORT is a proxy of food availability and energetic challenge in seabirds (Kitaysky et al. 2007). Furthermore, reproductive success of Hg-exposed tree swallows declined only under warm conditions, which could be mediated by disruption of THs and thermoregulatory capacity (Hallinger & Cristol 2011).

Effects of climate change and contaminants on energy allocation may be especially pronounced in long-lived species which facultatively skip breeding. Frequency of skipping breeding increases in red-footed boobies (*Sula sula*) in El Niño years (Cubaynes et al. 2011), and common murrelets (*Uria aalge*) in winters with high sea surface temperature (Reed et al. 2015), with both phenomena predicted to increase with climate change. Contaminated seabirds, such as Hg-exposed black-legged kittiwakes, also skip breeding more often (Tartu et al. 2013). Deteriorating conditions for breeding and concomitant increases in contaminant exposure or toxicity might additively or synergistically reduce breeding incidence and population stability, with synergistic effects potentially induced if the combination of the two stressors caused organisms to surpass a threshold past which breeding activity could not be sustained.

Increased reproductive investment. Conversely, contaminated individuals might maladaptively sustain reproductive effort under poor conditions, compromising energy balance and survivorship. Behavioral

adjustments promoting self-maintenance over reproduction are mediated by elevation of GCs in vertebrates (McEwen & Wingfield 2003; Tartu et al. 2013). These responses are often adaptive, and could stabilize populations. Contaminated individuals could have a reduced threshold for downregulating reproduction, mediated by increased HPA activity. However, both Hg and POPs can reduce HPA sensitivity (Box 2). For example, Hg-exposed tree swallows displayed suppressed adrenocortical stress responses (Wada et al. 2009), which could increase the threshold for abandoning reproduction under environmental stress. Contaminant exposure could also trigger increased reproductive investment by accelerating senescence and inducing terminal reproductive effects (Koivula & Eeva 2010; Dietz et al. 2019). These effects could be exacerbated by climate change-driven effects, such as increased environmental challenge or altered growth trajectories (Burraco et al. 2020).

Reduced energetic costs. Climate change-linked decreases in thermoregulatory costs at high latitudes could counterbalance effects of diminished resource supply on the survival-reproduction tradeoff, allowing maintenance of reproductive effort, even given synergistic effects of resource shortage and contamination on energy supply. Indeed, warming Arctic temperatures reduced thermoregulatory costs for dunlin (*Calidris alpina*) chicks, allowing sustained growth despite reduced resource availability (McKinnon et al. 2013). Reduced thermoregulatory costs could favor increased reproductive effort, potentially with self-maintenance costs, but feasibility of upregulating reproductive effort could decline with contamination.

Energy management strategy

Interfering with EMS. Organisms can adjust the EMS through which they balance investment into BMR, AEE and DEE depending on energy availability and physiological state (Careau & Garland 2012; Halsey et al. 2019). Abundant resources may enable an independence or performance EMS. In independent energy management, no restriction on energy expenditure exists, and BMR and activity additively affect DEE. BMR does not covary with activity and positively covaries with DEE. In performance energy management, an intrinsic positive association between BMR, activity and DEE exists, and upregulating

BMR mobilizes energy for activity. Conversely, given resource shortage or intense energy demand, a limit to DEE is approached, inducing a BMR-activity tradeoff, and constrained energy management, in which BMR and DEE do not covary (Careau & Garland 2012; Halsey et al. 2019).

Contaminant exposure may interfere with animals' capacity to manage energy use given climate change-associated challenges. First, contaminant-linked increases in BMR could prevent downregulation of BMR and constrained energy management (Fig. 3a), deeming individuals unable to compensate for energy shortage, and forcing reduced reproductive investment (Fig. 3a). In incubating black-legged kittiwakes, a decrease in BMR before hatching decreases investment into self-maintenance and increases investment into chick provisioning (Blévin et al. 2017). As aforementioned, kittiwakes exposed to PFASs displayed elevated BMR, which could compromise ability to downregulate BMR and increase reproductive investment (Blévin et al. 2017). Several studies on Arctic seabirds (although not Blévin et al. 2017) document positive relationships between PFASs and THs (e.g. Ask et al. 2021), suggesting that thyroid disruption could mediate changes in metabolism and behavior (Box 1). If climate change increases energetic costs of incubation, or resource limitation, inability to modulate BMR to conserve energy could become increasingly problematic. Conversely, contaminant-linked suppression of BMR might interfere with upregulation of BMR and performance energy management (Fig. 3b). If birds must feed chicks at higher rates to compensate for reduced prey quality (Senécal et al. 2021), or increase foraging time to maintain provision rates at low prey density (Harding et al. 2007), importance of performance energy management could increase.

Furthermore, contaminant exposure might affect when individuals adopt different EMSs. For example, contaminant exposure might magnify effects of climate change-linked energy shortages, such that contaminated individuals with elevated BMRs reach a threshold in DEE and switch between independent/performance and constrained EMSs at lower AEE, and spend more time employing constrained energy management (Fig. 4), potentially reducing fitness.

Future directions

We currently lack clear understanding regarding which contaminant-by-environment interactive effects result in broad-scale changes in population and ecosystem dynamics. To build a comprehensive understanding of bioenergetic outcomes and predict large scale responses, we particularly encourage research in the following areas.

How do lower level effects (e.g. on MR) combine to affect higher bioenergetic (e.g. DEE) and fitness

traits? Effects exerted across multiple lower level bioenergetic processes, such as BMR and activity, might combine to determine higher level effects on energy balance, DEE, and fitness. First, effects of contamination on lower level traits could combine to amplify higher level effects (Fig. 5a). Conversely, effects on lower level traits could counteract one another, dampening higher level effects (Fig. 5b). In either case, considering effects on multiple traits will aid in predicting energetic outcomes.

Which species, populations, individuals? Vulnerable species' responses will serve as fulcrums around which broader-scale contaminant-by-environment interactive effects become manifest. Thus, identifying traits that determine vulnerability is essential. High trophic level species experience biomagnification (Burger & Gochfeld 2004; Michelutti et al. 2010), and may be more sensitive to contaminant-induced effects on bioenergetics. Species also differ in evolved detoxification mechanisms, affecting sensitivity to contamination (Ikemoto et al. 2004). Furthermore, vulnerability may be higher in long-lived species due to bioaccumulation (Burger & Gochfeld 2004), and in species and populations occupying habitats or areas that serve as contaminant sinks (e.g. the Arctic; agricultural fields). Individuals may also differ in contaminant exposure due to feeding specialization and differences in spatial movement (Saaristo et al. 2018; Leat et al. 2019).

With respect to sensitivity to climate change, vulnerability may be elevated in species inhabiting regions experiencing rapid change (e.g. polar regions), environments close to thermal tolerance limits, or areas lacking options for spatiotemporal shifts in range or phenology (Parmesan 2006). Range-edge populations may be pre-adapted to cope with climatic extremes (Rehm et al. 2015), but may also suffer from reduced genetic diversity, potentially limiting scope for genetic response (Eckert et al. 2008).

Overlap between high vulnerability to contaminant- and climate-related stress will determine species and

populations of concern. Finally, determining physiological, behavioral and energetic characteristics that heighten sensitivity once exposure occurs will be important.

When and over which timescales? Vulnerability to contaminant-by-environment interactive effects may increase during energy-intensive life history stages, or periods of environmental challenge, including winter at high latitudes (Fort et al. 2009, 2015). Research demonstrates shifts in spatiotemporal variation in energy balance with climate change-associated environmental variation (Amélineau et al. 2018; Clairbaux et al. 2021). Contaminant exposure now needs to be integrated into models. Contaminant exposure may be concentrated during particular times of the year or life history stages (Fort et al. 2014). Exposure may be higher on breeding or wintering grounds (Albert et al. 2021), and effects may increase with age due to bioaccumulation (Burger & Gochfeld 2004). Studies are needed that span annual cycles and lifespans, and explore timeframes over which effects operate. There could also be lag-times between exposure and when effects become manifest, meaning that stressors need not occur simultaneously to produce interactive effects (Jackson et al. 2021). The timeframe of stress exposure (e.g. pulse versus press disturbance; Bender et al. 1984) could also affect the nature of effects, and scope for evolutionary response. Finally, more research is needed on transgenerational effects of contaminants and environmental stress exposure. For instance, contaminant exposure may impact organisms' capacity to respond to climate change across multiple generations through epigenetic alterations in the germline that promote inheritance of disease (Beck et al. 2022).

Indirect trophic effects? Even organisms physiologically resistant to contaminant exposure or climate change may suffer effects via indirect pathways (Saaristo et al. 2018). Climate change is restructuring food webs, affecting how impacts of contaminants on one species propagate to affect others. For instance, global warming is transforming Arctic marine food webs by introducing boreal generalist fish, reducing modularity and increasing connectivity. Reduced modularity increases propagation of perturbations, such as contaminants, through food webs (Kortsch et al. 2015).

Thresholds and other non-linearities? Reaction norms describing effects of contaminant exposure and environmental stress on energetic traits may be non-linear. Negligible effects may occur below thresholds

of contamination that challenge detoxification mechanisms, or within the range of environmental conditions encompassed by acclimatization responses (Fisk et al. 2005). Beyond these thresholds, energetic responses may range in form from linear to exponential, and plasticity's ability to buffer fitness may be surpassed. Research is needed to establish whether contaminant exposure lowers thresholds at which organisms become vulnerable to environmental change, and *vice versa*. In addition to thresholds, other non-linearities in the impact of contaminant exposure or environmental stress deserve further attention, as they will complicate the nature of interactive effects. Examples include inverse dose-response curves (Vandenberg et al. 2012), and hormetic effects (Sebastiano et al. 2022).

Conclusions Climate change and contaminant exposure can have wide-ranging effects on bioenergetic traits. These effects may be additive in nature, but substantial evidence exists for both synergistic and antagonistic interactive effects. Our review revealed relative balance between antagonistic and synergistic interactions, and like other recent syntheses, suggested that unpredictable, non-additive interactions are more common than additive effects (e.g. Crain et al. 2008; Darling & Côté 2008). Prevalence of synergistic interactions was once emphasized, but it has now been suggested that synergies do not prevail among interaction types (Darling & Côté 2008; Côté et al. 2016). However, addition of a third stressor can increase prevalence of synergies (Crain et al. 2008), and different studies may employ different null models, which can affect the interaction types observed (Côté et al. 2016). Synergistic interactions are often construed as particularly problematic, since they magnify effects on focal traits. Consequentially, some have argued that conservation actions should target synergies (Côté et al. 2016; Arrigo et al. 2020). However, for bioenergetic traits, antagonistic interactions may be equally deleterious, since they can reflect suppression of responses that facilitate energy balance. Moreover, an antagonistic interaction on a bioenergetic trait may translate into a synergistic effect on reproductive success or survivorship, and interactive effects on multiple traits may act jointly to amplify or reduce fitness effects. Research on contaminant-by-climate change interactive effects on free-living organisms remains limited, with a notable shortage of research on endotherms, and Arctic endotherms in particular. Especially for these taxa, we have limited latitude to suggest which types of interactive effects are most important. However,

Arctic endotherms may be highly vulnerable to diverse climate change-by-contaminant interactive effects due to rapid warming and shifts in contaminant exposure. Predicting future ramifications of climate change and contaminant exposure on Arctic ecosystems, and globally, will depend on understanding mechanistic underpinnings of interactive effects, and how different effects will combine to affect fitness, species interactions, and community dynamics.

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TABLES

Table 1. Summary of organisms, contaminant types, and environmental stressors encompassed, and contaminant-by-environment interactive effects reported, by empirical studies. Some studies involved multiple types of contaminants, environmental stressors and classes of interactive effects. Numbers for interactive effect classes refer to the number of studies reporting such an effect, but some studies may have reported the same type of effect for multiple variables. Some studies did not statistically test the interactive effect (e.g. because separate experiments were conducted under two conditions or only a one-way ANOVA was used). Of these studies, graphical depictions of results mostly allowed verification that the interactive effect was significantly different than the additive prediction. However, in a few cases this was difficult. We note these cases in parentheses when reporting classes of interactive effects. See Supplementary Material for the methodology of the literature review.

Bioenergetic domain	Sub-domain	Organism type			Ecosystem type		Contaminant type				Environmental stressors				Interactive effects (difficult to compare to additive prediction)				
		END	ECV	ECIV	Arctic (of which END)	OTH	MET	POP	CEAC	OTH	RA	T	PRD	PAR	NS	PS	NA	PA	Null/ADD
Energy supply	Foraging	7	7	11	3(3)	11	11	4	1	9	13	6	5	1	7(3)	2(1)	5(1)	2(1)	13
Energy supply	Assimilation/ Metabolic Efficiency	0	3	5	0	8	3	3	1	1	0	5	2	1	4	0	2	0	3
Energy demand	Metabolism	4	15	39	1(0)	58	37	6	2	15	4	49	2	2	8	8	16	12	22
Energy demand	Thermo-regulation	4	3	21	1(1)	27	3	2	10	14	5	25	1	1	7(4)	5(2)	4(1)	6(2)	8
Energy demand	Activity	2	17	15	0	34	8	5	6	14	1	21	10	2	6	6	9	4	18
Energy demand	Immune defense	4	7	19	2(1)	28	18	6	2	4	1	14	2	13	5	11(1)	3	5	19
Energy storage	Energy storage	2	12	25	0	39	20	3	9	8	2	31	3	6	8(1)	5	5	3	29
Total		23	64	135	7(5)	205	100	29	31	65	26	151	25	26	45	37	44	32	112

END= endotherm, ECV= ectotherm vertebrate, ECIV= ectotherm invertebrate, MET= metal, POP= POP, CEAC= other contaminant of emerging Arctic concern, OTH= other, RA= resource availability, T= temperature, PRD= predation risk, PAR= parasitism, NS= negative synergy, PS= positive synergy, NA= negative antagonism, PA= positive antagonism, Null= non-significant

FIGURE LEGENDS

Figure 1. The effects of climate change-associated stressors and contaminants on bioenergetic traits may be additive, with individuals differing in contaminant load displaying parallel reaction norms across environmental gradients. Alternatively, effects may be interactive. First, contamination may modify the slope of reaction norms with respect to climate-change associated stressors, as proposed by toxicant-induced climate sensitivity (Hooper et al. 2013). For example, as temperature increases endotherms may decrease metabolic rate to conserve energy, but this response may be dampened if detoxification costs elevate metabolic rate (a). Here, since metabolic rate changes less steeply with environmental conditions within more contaminated individuals, antagonistic (<additive) effects result. Note that metabolic rate may be modified when temperature either increases or decreases away from an optimal temperature, or temperature range (thermal neutral zone), and contamination might interfere with such modulation. Additionally, climatic stress may alter effects of contamination on bioenergetic traits, as proposed by climate-induced toxicant sensitivity (Hooper et al. 2013) (b). Here, metabolic rate increases more steeply with contaminant exposure at higher temperatures, which could reflect heightened toxicity and detoxification costs, resulting in synergistic (>additive) effects. Note that climate-driven and contaminant-driven processes in reality operate simultaneously, as visualized by reaction norms in three-dimensional space (c). We consider the potential for such interactive effects within five bioenergetic domains. These processes may affect fitness outcomes, especially in challenging environments (bottom).

Figure 2. Framework for classifying interactive effects between stressors when effects are in the a) same or b) opposite directions. Single stressor effects (E1 and E2) appear below the horizontal line, and cumulative effects classified as additive (Add), antagonism (Ant), synergy (Syn), or dominant (Dom) above. Given effects in the same direction and an additive null model (vertical line in a), classifying effects as antagonism or synergy (less or more in absolute value than the additive prediction) is straightforward. Given effects in opposing directions, classification becomes contentious. We classified

interactive effects as antagonism if less in absolute magnitude than the single stressor effect in the same direction (outer vertical lines in b). The effect is called positive antagonism if more negative than the additive prediction (positive effect antagonized), and negative antagonism if more positive than the additive prediction (negative effect antagonized). Some have instead labelled effects greater in magnitude than the additive prediction and in the same direction synergy (negative antagonism bar in b). We classified effects as synergy only given an absolute magnitude greater than the single stressor effect in the same direction. The effect was called positive synergy if greater than a positive single stressor effect, and negative synergy if less than a negative single stressor effect. Dominant effects are of the same magnitude as one of the single stressor effects, and can also be viewed as a form of antagonism (other stressor effect is antagonized). Framework derived from Piggott et al. 2015.

Figure 3. Hypothetical relationships in individuals with high, versus low, contamination loads between (a) auxiliary energy demand and BMR (top) and activity (bottom), given constrained energy management and elevation of BMR by detoxification costs, and (b) auxiliary energy demand and BMR (top) and activity or FMR (bottom), given performance energy management and suppression of BMR by contamination.

Figure 4. Hypothetical relationship between contaminant exposure and time of switching between independent/performance and constrained energy management. When DEE is below a threshold (dashed line, a), auxiliary energy expenditure (AEE) is unconstrained by maintenance energy expenditure (BMR), or *vice versa*. As AEE increases, a threshold is reached, and reductions in AEE constrain DEE. Here, highly contaminated individuals (HC) have higher maintenance costs (BMR), surpass the threshold at lower AEE than individuals with low contamination loads (LC), and switch strategies sooner. The slope of the DEE-BMR relationship for the entire period (b) lies between 1 and 0 for both types of individuals, indicating partial energy constraint. However, the slope for HC individuals is closer to 0, indicating greater constraint. Contaminated individuals might also switch between an independent/performance

EMS and constrained EMS at a lower threshold of DEE (imagine shifting the dashed line in a) down, but only for contaminated individuals), which could accentuate the difference in time between when contaminated and uncontaminated individuals switch. Extended from figure 2 of Halsey et al. 2019.

Figure 5. Hypothetical example of reaction norms in multiple bioenergetic traits combining to determine reaction norms in higher level traits. Polar bears exhibit a seasonal fast during the summer and fall when sea ice disappears, whose duration is increasing with climate change. Simultaneous reductions in BMR and activity allow bears to reduce DEE (a; reaction norms in solid black) and survive the fast (Stirling & Derocher 2012). However, contaminant exposure might interfere with both responses (a; reaction norms in dashed red) by elevating basal detoxification costs and causing hyperactivity through endocrine-disrupting effects (e.g. PDBEs cause hyperactivity in rats; Suvorov et al. 2009), especially as contaminants are released from lipid reserves in fasting bears (Polischuk et al. 2002), resulting in sustained elevated DEE, and deleterious effects on survival. Alternatively, reaction norms in one lower level trait may buffer against lack of response in another, maintaining the response in the higher level trait (b). For instance, if contaminated polar bears with heightened detoxification costs are unable to suppress BMR, activity levels may be more dramatically reduced than in uncontaminated individuals, such that a similar reaction norm in DEE is observed in contaminated and uncontaminated individuals, potentially serving as an adaptive buffering response to prevent starvation.