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

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3 **Climate change, contamination, bioenergetics**

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16

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

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

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

36
37 **INTRODUCTION** Unprecedented shifts in abiotic and biotic conditions related to climate change pose
38 energetic challenges, including direct effects on metabolism and thermoregulation (Dillon et al. 2010) and
39 indirect effects mediated via trophic dynamics and resource supply (Bartley et al. 2019). Given limited
40 energy budgets, maintaining optimal function under shifting conditions involves differential balance of
41 energetic trade-offs (Norin & Metcalfe 2019). Plasticity may facilitate adaptation (Seebacher et al. 2015),
42 and microevolutionary change may move populations towards new optima (Parmesan 2006; Karell et al.
43 2011; Norin & Metcalfe 2019). Predicting bioenergetic effects of climate change is a current area of
44 intense research interest (Dillon et al. 2010; Magozzi & Calosi 2015; Clairbaux et al. 2021).

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

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

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

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

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

79 2022). Although isolated from contamination sources, the Arctic acts as a sink for volatile contaminants,
80 which persist in cold environments and increase in concentration at higher trophic positions through
81 biomagnification (AMAP 2021a,b). Although levels of legacy POPs (e.g. PCBs) show decreasing trends
82 in the Arctic, these trends are slowing or leveling off, and other POPs (e.g. PBDEs) are often increasing,
83 as are chemicals of emerging Arctic concern (CEAC; e.g. per- and polyfluoroalkyl substances (PFASs);
84 flame retardants). Another important contaminant in the Arctic, mercury (Hg), displays decreasing
85 atmospheric trends, but both increasing and decreasing trends have been observed in biota (AMAP
86 2021a). Thus, cumulative contaminant impacts are likely to increase in the Arctic in coming decades
87 (AMAP 2021b). We used the Arctic Monitoring and Assessment Programme report, listing contaminants
88 of concern in the Arctic (AMAP 2021), to guide our literature search (Supplementary Material for
89 details). Given the few studies assessing interactive effects on Arctic organisms (Table 1), we expanded
90 our review to encompass all animal taxa, while frequently incorporating discussions of how interactive
91 effects might affect Arctic endotherms.

92

93 **INTERACTIVE EFFECTS ACROSS BIOENERGETIC DOMAINS**

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

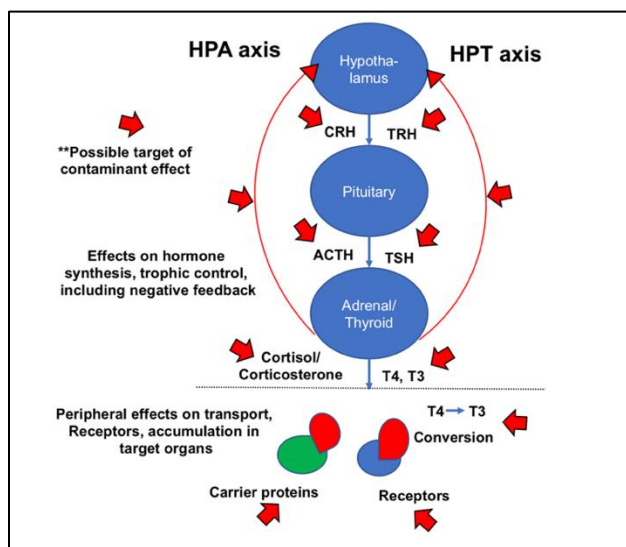
101 **Energy supply**

102 ***Foraging and ingestion***

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

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

114
 115 **Box 1. Endocrine pathways through which contaminants may disrupt metabolism:** Contaminants
 116 can interfere with physiological mechanisms, including the hypothalamus-pituitary-adrenal (HPA) and
 117 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

126 thyroid stimulating hormone (TSH) (De Groef et al. 2006). The HPT axis mediates oxygen consumption,
 127 ATP use, and thermogenesis through release of THs, thyroxine (T₄), and 3,5,3-triiodothyronine (T₃) (Yen
 128 2001; Leemans et al. 2019; Ruuskanen et al. 2021).

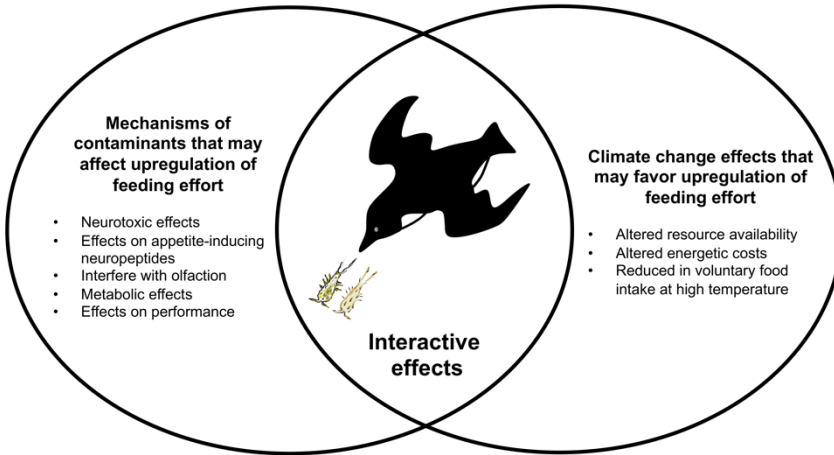
129 Contaminants affect hormonal axes via diverse mechanisms, including interference with receptors,
 130 carrier proteins, hormone release or negative feedback. Metal- and POP-exposure can both elevate GCs

131 and suppress HPA sensitivity (Tartu et al. 2014; Monclús et al. 2018). OC- and PCB-exposure may
132 decrease THs via direct action on the thyroid, interfering with transport proteins, or disrupting
133 deiodinases, such as those converting T₄ to T₃ (Wada et al. 2009; Leemans et al. 2019). Conversely,
134 PFASs have been positively associated with THs (Melnes et al. 2017; Ask et al. 2021). In black-legged
135 kittiwakes (*Rissa tridactyla*), PFASs positively correlated with T₄ in males and T₃ in females, with the
136 mechanism involving competition with THs for binding proteins (e.g. albumin). Increased THs could
137 elevate BMR, interfere with thermal acclimation and reduce tolerance to cold or heat (Ask et al. 2021).
138

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

153

154 **Box 2. Mechanisms of contaminant-linked effects on upregulation of foraging effort:** Neurotoxic
 155 effects can compromise locomotion, reducing foraging efficiency (Kobiela et al. 2015; Ecke et al. 2017).
 156 Contaminant exposure can also affect foraging motivation through actions on appetite-inducing or
 157 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).

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

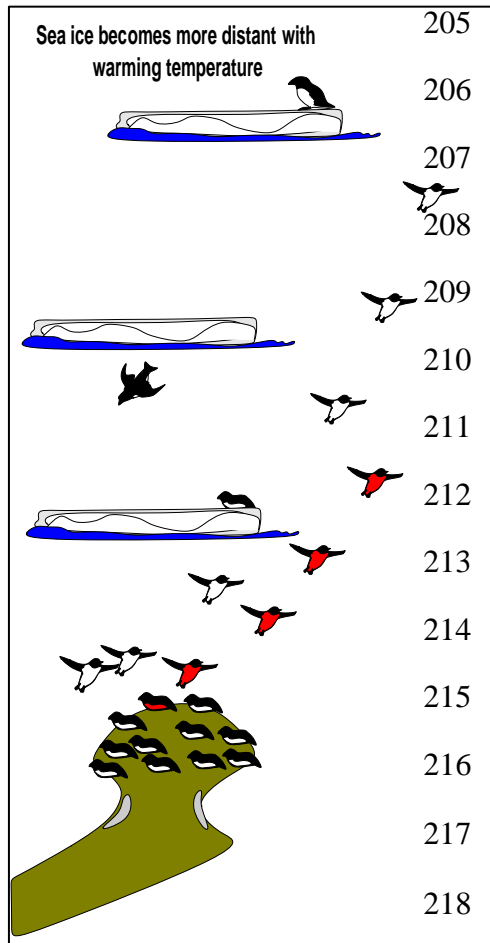
174
 175 Examples of contaminant-by-resource availability interactive effects in endotherms include a study on
 176 Arctic thick-billed murres (*Uria lomvia*) exposed to Hg, which displayed altered T_3 only during years
 177 with suboptimal conditions associated with advanced sea ice breakup. Elevated T_3 was associated with
 178 reduced diving, which could result in negative synergistic effects on energy intake (Esparza et al. 2022).

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

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

190 Contamination could also affect animals' ability to phenologically track shifting resource peaks, for
191 instance by deeming individuals unable to advance breeding under warmer conditions (Charmantier et al.
192 2008). Evidence exists of contaminated birds delaying egg laying date (Helberg et al. 2005; Bustnes et al.
193 2007), but interactive effects with environmental conditions remain largely unexplored. One study
194 reported a non-intuitive result. Common eiders (*Somateria mollissima*) laid later in warmer years, with this
195 effect less pronounced in Hg-exposed females (Smith et al. 2022). The mechanism underlying this effect
196 was postulated to involve disruption of the HPA axis by Hg (Smith et al. 2022).

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

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

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

253

254 *Assimilation and metabolic efficiency*

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

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

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

277

278 **Energy demand**

279 *Metabolism*

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

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

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

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

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

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

314

315 ***Thermoregulation***

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

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

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

335 Mechanistically, contaminant-by-temperature interactive effects on thermoregulation may reflect
336 disrupted acclimatization responses. For instance, small birds overwintering in temperate zones employ
337 facultative hypothermia to conserve energy (McKechnie & Lovegrove 2002), and increase cold tolerance
338 by elevating BMR and reducing thermal conductance (Douglas et al. 2017). Endotherms also display
339 facultative hyperthermia to reduce need for water to drive evaporative cooling (Hetem et al. 2014;
340 Douglas et al. 2017; Gerson et al. 2019b). On a related vein, endotherms can adjust heat dissipation
341 capacity to maintain optimal function (Speakman 2018). In lieu of effective heat dissipation,
342 hyperthermia results, which can damage proteins, induce oxidative stress or be fatal (Speakman & Król
343 2010; Tapper et al. 2020; Rogers et al. 2021). Heat dissipation capacity has strong effects during energy-
344 intensive life-history stages, such as lactation (Speakman & Król 2010; Zhao et al. 2020), or nestling
345 provisioning (Tapper et al. 2020), and may limit DEE in Arctic animals adapted to retain heat (Blix 2016),
346 and large animals with low surface area to volume ratios (Rogers et al. 2021). Box 4 discusses
347 physiological mechanisms that could underlie disruption of thermoregulatory responses by contaminants,
348 generating interactive effects.

349 Projected gradual increases in mean temperatures are within the range of acclimatization responses,
350 and may not result in thermal stress (McKechnie 2008), especially at high latitudes (Fort et al. 2009;
351 Amélineau et al. 2019). However, adjustments in BMR and body temperature can occur between and
352 within days (McKechnie 2008). Thus, climate change-linked increases in temperature fluctuations and
353 extreme weather (Meehl & Tebaldi 2010) could increase potential for contaminant-linked changes in
354 BMR and thermal setpoints to compromise energy balance. Furthermore, at higher temperatures,
355 increasing detoxification costs, bioavailability and toxicity, and cellular damage related to heat stress
356 could cause synergistic increases in BMR and thermal challenge (Verreault et al. 2007; Hooper et al.
357 2013). Conversely, warmer temperatures sometimes increase contaminant clearance (Noyes et al. 2009),
358 which might ameliorate detoxification costs, reduce BMR, and generate antagonistic effects.

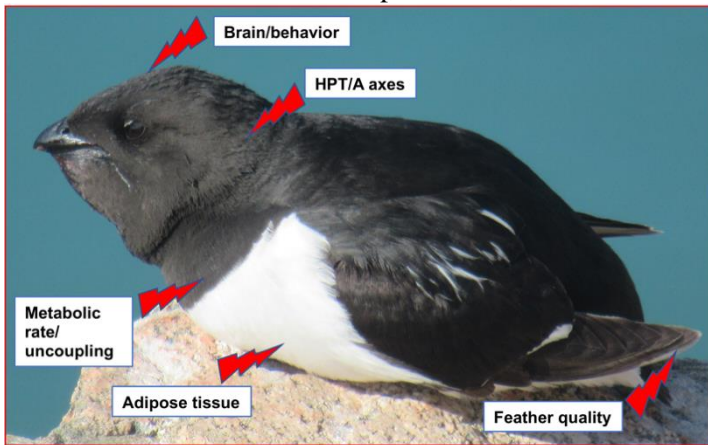
359 *Other types of contaminant-by-environment interactive effects on thermoregulation.* Contaminant
360 exposure might also interact with environmental variables besides temperature to affect thermoregulation
361 (Table 1, S5). For example, a positive synergistic interaction occurred between radioactivity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

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

385

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

387 Contaminant exposure may interfere with thermoregulation via endocrine disruption, with effects on the
388 HPT axis particularly relevant, due to its role in mediating thermoregulation in vertebrates (Verreault et
389 al. 2004, 2007; Wada et al. 2009). Contaminants could also impact thermoregulation via effects on body
390 composition (more lean versus adipose tissue) and the integument (feather, fur quality). Contaminated
391 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 increases, generating an
antagonistic effect on body temperature and

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

410

411 ***Physical activity***

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

417 *Contaminant-by-temperature interactive effects on activity.* Eleven studies (one on endotherms) reported
418 significant contaminant-by-temperature interactive effects on activity, with no one interaction type clearly
419 dominating. For instance, female mice (*Mus musculus*) prenatally exposed to methylmercury showed
420 inactivity during an open field test, but this effect was dampened in combination with thermal stress,
421 resulting in negative antagonism (Yin et al. 1997). Different types of contaminant-by-temperature
422 interactive effects on activity are predicted to have distinct implications for energy balance. For example,
423 rising temperatures can elevate activity-related energy costs in endotherms. Heat generated by activity
424 offsets thermoregulatory costs under cold conditions (Careau & Garland 2012), but must be dissipated as
425 temperature rises, via vasodilation and evaporative water loss (McKechnie & Wolf 2019; O'Connor et al.
426 2021). Thus, thermally-stressed organisms may downregulate activity to conserve energy and water, a
427 strategy that may be disrupted by negative antagonistic or positive synergistic interactive effects with
428 contaminants. Conversely, increasing temperature may increase performance, especially in ectotherms,
429 and this effect may be dampened via positive antagonistic interactions with contamination (e.g. Quiroga
430 et al. 2019).

431 *Contaminant-by-predation risk interactive effects on activity.* Seven studies on ectotherms (no studies
432 exist on endotherms) reported negative antagonistic interactions between contaminant exposure and
433 predation risk (Table 1, S6). For example, metal-exposed round goby (*Neogobius melanostomus*)
434 downregulated activity less than unexposed individuals under predation risk (Marentette & Balshine
435 2012). A similar effect could be classified as positive synergy, if activity in contaminated individuals
436 under predation risk is greater than the additive prediction (e.g. Preston et al. 1998; Janssens & Stoks

437 2012). As for foraging, this interactive effect could reflect neurological effects of contaminants that
438 promote hyperactivity, or need to maintain high energy intake to cover detoxification costs. Sustained
439 activity under predation risk could have fitness implications. For example, in the rotifer (*Brachionus*
440 *calyciflorus*), pentachlorophenol exposure reverses adaptive decreases in swimming speed that reduce
441 predator encounters rate, with exposed *B. calyciflorus* displaying an ~30% increase in swimming speed in
442 presence of the predatory rotifer (*Asplanchna girodi*), elevating predation risk by ~50% (Preston et al.
443 1998). In contrast, a negative synergistic effect between predation risk and contaminant exposure was
444 observed in wolf spiders (*Pardosa milvina*), which only reduced movement in response to cues from
445 predatory carabid beetles (*Scarites quadriceps*) if exposed to a glyphosate-based herbicide (Wrinn et al.
446 2012).

447

448 ***Immune defense***

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

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

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

474

475 **Energy storage**

476 The balance between energy supply and demand affects energy storage capacity, which is critical during
477 particular life history stages, such as prior to migration or hibernation (Guglielmo 2018; Weitten et al.
478 2018), before breeding in capital breeders (Gauthier et al. 2003), and in animals preparing for winter
479 resource scarcity (Blix 2016). Since certain diets promote or hinder fatty acid synthesis (Weitten et al.
480 2018), climate change-related shifts in resource availability may be detrimental to energy storage.

481 Scarcity of essential food resources during critical periods may force animals to use alternative resources,
482 or increase spatiotemporal scope of foraging effort. Contaminant exposure may combine with climate
483 change-related effects on energy storage through a variety of mechanisms (Box 5).

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

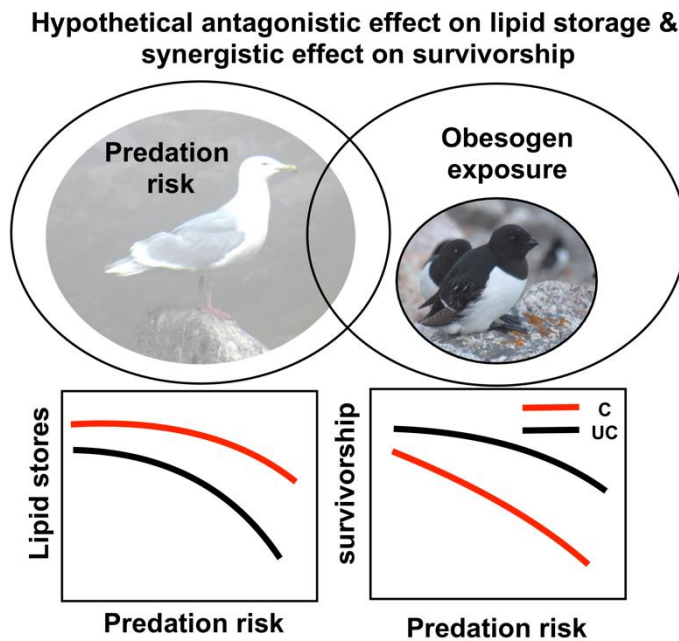
489 increased risk sensitivity (Kobiela et al. 2015). Given climate change-linked elevation in predation risk,
490 such an effect could further undermine contaminated organisms' ability to store energy.

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

500

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

502 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

513 in humans (Grün & Blumberg 2009), and inappropriate weight gain in animals (Martinson & Fernie

514 2019). Obesogens have potent effects early in life, predisposing individuals to altered metabolic profiles

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

527

528 **Energy allocation**

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

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

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

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

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

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

567 adjustments promoting self-maintenance over reproduction are mediated by elevation of GCs in
568 vertebrates (McEwen & Wingfield 2003; Tartu et al. 2013). These responses are often adaptive, and could
569 stabilize populations. Contaminated individuals could have a reduced threshold for downregulating
570 reproduction, mediated by increased HPA activity. However, both Hg and POPs can reduce HPA
571 sensitivity (Box 2). For example, Hg-exposed tree swallows displayed suppressed adrenocortical stress
572 responses (Wada et al. 2009), which could increase the threshold for abandoning reproduction under
573 environmental stress. Contaminant exposure could also trigger increased reproductive investment by
574 accelerating senescence and inducing terminal reproductive effects (Koivula & Eeva 2010; Dietz et al.
575 2019). These effects could be exacerbated by climate change-driven effects, such as increased
576 environmental challenge or altered growth trajectories (Burraco et al. 2020).

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

585

586 **Energy management strategy**

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

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

596 Contaminant exposure may interfere with animals' capacity to manage energy use given climate
597 change-associated challenges. First, contaminant-linked increases in BMR could prevent downregulation
598 of BMR and constrained energy management (Fig. 3a), deeming individuals unable to compensate for
599 energy shortage, and forcing reduced reproductive investment (Fig. 3a). In incubating black-legged
600 kittiwakes, a decrease in BMR before hatching decreases investment into self-maintenance and increases
601 investment into chick provisioning (Blévin et al. 2017). As aforementioned, kittiwakes exposed to PFASs
602 displayed elevated BMR, which could compromise ability to downregulate BMR and increase
603 reproductive investment (Blévin et al. 2017). Several studies on Arctic seabirds (although not Blévin et al.
604 2017) document positive relationships between PFASs and THs (e.g. Ask et al. 2021), suggesting that
605 thyroid disruption could mediate changes in metabolism and behavior (Box 1). If climate change
606 increases energetic costs of incubation, or resource limitation, inability to modulate BMR to conserve
607 energy could become increasingly problematic. Conversely, contaminant-linked suppression of BMR
608 might interfere with upregulation of BMR and performance energy management (Fig. 3b). If birds must
609 feed chicks at higher rates to compensate for reduced prey quality (Senécal et al. 2021), or increase
610 foraging time to maintain provision rates at low prey density (Harding et al. 2007), importance of
611 performance energy management could increase.

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

617

618 **Future directions**

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

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

629 ***Which species, populations, individuals?*** Vulnerable species' responses will serve as fulcrums around
630 which broader-scale contaminant-by-environment interactive effects become manifest. Thus, identifying
631 traits that determine vulnerability is essential. High trophic level species experience biomagnification
632 (Burger & Gochfeld 2004; Michelutti et al. 2010), and may be more sensitive to contaminant-induced
633 effects on bioenergetics. Species also differ in evolved detoxification mechanisms, affecting sensitivity to
634 contamination (Ikemoto et al. 2004). Furthermore, vulnerability may be higher in long-lived species due
635 to bioaccumulation (Burger & Gochfeld 2004), and in species and populations occupying habitats or areas
636 that serve as contaminant sinks (e.g. the Arctic; agricultural fields). Individuals may also differ in
637 contaminant exposure due to feeding specialization and differences in spatial movement (Saaristo et al.
638 2018; Leat et al. 2019).

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

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

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

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

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

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

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

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

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1380 **TABLES**

1381 **Table 1.** Summary of organisms, contaminant types, and environmental stressors encompassed, and contaminant-by-environment interactive
 1382 effects reported, by empirical studies. Some studies involved multiple types of contaminants, environmental stressors and classes of interactive
 1383 effects. Numbers for interactive effect classes refer to the number of studies reporting such an effect, but some studies may have reported the same
 1384 type of effect for multiple variables. Some studies did not statistically test the interactive effect (e.g. because separate experiments were conducted
 1385 under two conditions or only a one-way ANOVA was used). Of these studies, graphical depictions of results mostly allowed verification that the
 1386 interactive effect was significantly different than the additive prediction. However, in a few cases this was difficult. We note these cases in
 1387 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

1388 END= endotherm, ECV= ectotherm vertebrate, ECIV= ectotherm invertebrate, MET= metal, POP= POP, CEAC= other contaminant of emerging Arctic concern,
 1389 OTH= other, RA= resource availability, T= temperature, PRD= predation risk, PAR= parasitism, NS= negative synergy, PS= positive synergy, NA= negative
 1390 antagonism, PA= positive antagonism, Null= non-significant

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1395 **FIGURE LEGENDS**

1396

1397 **Figure 1.** The effects of climate change-associated stressors and contaminants on bioenergetic traits may
1398 be additive, with individuals differing in contaminant load displaying parallel reaction norms across
1399 environmental gradients. Alternatively, effects may be interactive. First, contamination may modify the
1400 slope of reaction norms with respect to climate-change associated stressors, as proposed by toxicant-
1401 induced climate sensitivity (Hooper et al. 2013). For example, as temperature increases endotherms may
1402 decrease metabolic rate to conserve energy, but this response may be dampened if detoxification costs
1403 elevate metabolic rate (a). Here, since metabolic rate changes less steeply with environmental conditions
1404 within more contaminated individuals, antagonistic (<additive) effects result. Note that metabolic rate
1405 may be modified when temperature either increases or decreases away from an optimal temperature, or
1406 temperature range (thermal neutral zone), and contamination might interfere with such modulation.
1407 Additionally, climatic stress may alter effects of contamination on bioenergetic traits, as proposed by
1408 climate-induced toxicant sensitivity (Hooper et al. 2013) (b). Here, metabolic rate increases more steeply
1409 with contaminant exposure at higher temperatures, which could reflect heightened toxicity and
1410 detoxification costs, resulting in synergistic (>additive) effects. Note that climate-driven and contaminant-
1411 driven processes in reality operate simultaneously, as visualized by reaction norms in three-dimensional
1412 space (c). We consider the potential for such interactive effects within five bioenergetic domains. These
1413 processes may affect fitness outcomes, especially in challenging environments (bottom).

1414

1415 **Figure 2.** Framework for classifying interactive effects between stressors when effects are in the a) same
1416 or b) opposite directions. Single stressor effects (E1 and E2) appear below the horizontal line, and
1417 cumulative effects classified as additive (Add), antagonism (Ant), synergy (Syn), or dominant (Dom)
1418 above. Given effects in the same direction and an additive null model (vertical line in a), classifying
1419 effects as antagonism or synergy (less or more in absolute value than the additive prediction) is
1420 straightforward. Given effects in opposing directions, classification becomes contentious. We classified

1421 interactive effects as antagonism if less in absolute magnitude than the single stressor effect in the same
1422 direction (outer vertical lines in b). The effect is called positive antagonism if more negative than the
1423 additive prediction (positive effect antagonized), and negative antagonism if more positive than the additive
1424 prediction (negative effect antagonized). Some have instead labelled effects greater in magnitude than the
1425 additive prediction and in the same direction synergy (negative antagonism bar in b). We classified effects
1426 as synergy only given an absolute magnitude greater than the single stressor effect in the same direction.
1427 The effect was called positive synergy if greater than a positive single stressor effect, and negative
1428 synergy if less than a negative single stressor effect. Dominant effects are of the same magnitude as one
1429 of the single stressor effects, and can also be viewed as a form of antagonism (other stressor effect is
1430 antagonized). Framework derived from Piggott et al. 2015.

1431
1432 **Figure 3.** Hypothetical relationships in individuals with high, versus low, contamination loads between
1433 (a) auxiliary energy demand and BMR (top) and activity (bottom), given constrained energy management
1434 and elevation of BMR by detoxification costs, and (b) auxiliary energy demand and BMR (top) and
1435 activity or FMR (bottom), given performance energy management and suppression of BMR by
1436 contamination.

1437
1438 **Figure 4.** Hypothetical relationship between contaminant exposure and time of switching between
1439 independent/performance and constrained energy management. When DEE is below a threshold (dashed
1440 line, a), auxiliary energy expenditure (AEE) is unconstrained by maintenance energy expenditure (BMR),
1441 or *vice versa*. As AEE increases, a threshold is reached, and reductions in AEE constrain DEE. Here,
1442 highly contaminated individuals (HC) have higher maintenance costs (BMR), surpass the threshold at
1443 lower AEE than individuals with low contamination loads (LC), and switch strategies sooner. The slope
1444 of the DEE-BMR relationship for the entire period (b) lies between 1 and 0 for both types of individuals,
1445 indicating partial energy constraint. However, the slope for HC individuals is closer to 0, indicating
1446 greater constraint. Contaminated individuals might also switch between an independent/performance

1447 EMS and constrained EMS at a lower threshold of DEE (imagine shifting the dashed line in a) down, but
1448 only for contaminated individuals), which could accentuate the difference in time between when
1449 contaminated and uncontaminated individuals switch. Extended from figure 2 of Halsey et al. 2019.

1450

1451 **Figure 5.** Hypothetical example of reaction norms in multiple bioenergetic traits combining to determine
1452 reaction norms in higher level traits. Polar bears exhibit a seasonal fast during the summer and fall when
1453 sea ice disappears, whose duration is increasing with climate change. Simultaneous reductions in BMR
1454 and activity allow bears to reduce DEE (a; reaction norms in solid black) and survive the fast (Stirling &
1455 Derocher 2012). However, contaminant exposure might interfere with both responses (a; reaction norms
1456 in dashed red) by elevating basal detoxification costs and causing hyperactivity through endocrine-
1457 disrupting effects (e.g. PDBEs cause hyperactivity in rats; Suvorov et al. 2009), especially as
1458 contaminants are released from lipid reserves in fasting bears (Polischuk et al. 2002), resulting in
1459 sustained elevated DEE, and deleterious effects on survival. Alternatively, reaction norms in one lower
1460 level trait may buffer against lack of response in another, maintaining the response in the higher level trait
1461 (b). For instance, if contaminated polar bears with heightened detoxification costs are unable to suppress
1462 BMR, activity levels may be more dramatically reduced than in uncontaminated individuals, such that a
1463 similar reaction norm in DEE is observed in contaminated and uncontaminated individuals, potentially
1464 serving as an adaptive buffering response to prevent starvation.