

1 **Captivity-induced metabolic programming in an endangered felid: implications**
2 **for species conservation**

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15 **Abstract**

16 Reintroduction of captive-bred individuals into the wild is an important conservation
17 activity. However, environmental conditions can influence developmental
18 programming, potentially causing metabolic disorders in adults. These effects are
19 investigated here for the first time in an endangered species. Using body weight and
20 feed intake data for Iberian lynx (*Lynx pardinus*) (n=22), we compared the growth of
21 captive versus wild born and/or reared individuals. Captive-born individuals gained
22 weight as a function of calorie intake, unlike wild-born individuals. When compared
23 with females reared in the wild, captive-reared females achieved a larger body size,
24 without evidence of obesity. Captivity-associated changes to metabolic programming
25 may compromise survival in the wild if an increased body size incurs a greater energy
26 requirement. Large body size may also confer a competitive advantage over smaller,
27 wild-born individuals, disrupting the social organisation of existing wild populations,
28 and potentially inferring long term implications for the phenotypic composition of wild
29 populations.

30 **Key words:** body condition, captive-breeding, carnivore, food intake, energetics, lynx,
31 reintroduction, nutrition

32 **Introduction**

33 The environmental and physiological conditions experienced by organisms during
34 sensitive periods of foetal and early post-natal development can exert profound effects
35 on individuals, including irreparable disruption to normal development or the
36 stimulation of alternative adult phenotypes, including those with increased susceptibility
37 to certain diseases^{1,2}. Controlled experiments with animals, as well as human
38 epidemiological studies, have demonstrated a developmental programming effect,
39 whereby early (pre- and post-natal) nutrition can influence metabolic processes in later

40 life, such as alterations to growth, glucose homeostasis, insulin sensitivity, energy
41 balance, lipid metabolism and obesity, as well as impairment of cardiac and endocrine
42 function ²⁻⁵. This metabolic programming may represent either a deleterious functional
43 impairment that arises from compromised development ⁶, or an adaptive response of the
44 foetus to the maternal environment that enables offspring to cope with the environment
45 to which they are exposed after birth ^{1,7}. Under the ‘coping’ hypothesis, challenges to
46 development, such as food deprivation, may be counteracted by short-term metabolic
47 changes ^{1,7}. These often carry longer-term fitness costs that present as impaired
48 physiological performance in the adult and may even persist into subsequent
49 generations ^{2,8,9}. Equally, the ‘developmental origins of health and disease’ concept,
50 which considers a range of potential mechanisms for metabolic programming, predicts
51 that disease prevention interventions implemented in adulthood (e.g. lifestyle changes in
52 exercise and diet) may be less effective for metabolically programmed individuals than
53 would be expected in the absence of such programming ⁷. Hence, factors that elevate
54 risk of poor health, including increased appetite, certain food preferences or reduced
55 propensity to exercise, may have more serious consequences in developmentally
56 programmed individuals ⁷.

57 In the context of endangered species conservation, a number of health and disease
58 concerns are known to uniquely affect captive populations. For example,
59 gastrointestinal disease is prevalent in captive cheetah (*Acinonyx jubatus*) populations,
60 but rarely detected in wild populations ¹⁰. Similarly, iron storage disease (ISD) and
61 obesity are captivity-specific conditions causing morbidity and mortality in a variety of
62 species; frugivorous and browsing avian and mammalian species are affected by ISD
63 ^{11,12}, and species ranging from lemurs (*Varecia* spp.) ¹³ to elephants (*Loxodonta*
64 *africana* and *Elephas maximus*) ¹⁴ are affected by diseases associated with obesity.

65 Captive breeding is increasingly utilised as a conservation action for endangered
66 species, but concerns about the genetic effects of domestication have been raised ¹⁵.
67 Whilst captive breeding programmes prioritise genetic diversity ¹⁶, there may be
68 unintended selection for certain phenotypic or genetic traits which may be beneficial in
69 captive environments but detrimental in free-living conditions ¹⁷, including genetic
70 effects that remain detectable after several generations ¹⁵. When captive bred animals
71 are used in reintroduction programmes, these effects can cause detrimental changes that
72 compromise post-release survival ¹⁵.

73 The key changes reported in captive bred animals, compared to wild conspecifics, are
74 alterations to behaviour ¹⁸⁻²⁰ and reproductive output ¹⁵. However, developmental
75 programming in response to nutritional stress may also result in metabolic rate
76 dysfunction in offspring ^{2,21,22}. While this has been explored in the laboratory by
77 manipulating the nutrient and energetic content of diets for rats (*Rattus norvegicus*
78 *domestica*) ^{23,24}, evaluation of the programming effect of rearing or birth environment is
79 less well understood.

80 The potential for metabolic programming effects are of particular concern for non-
81 domestic species since they typically experience greater food availability in captivity
82 compared to wild conspecifics ²⁵. An outcome of this high food availability is often an
83 alteration to the growth and development of animals in captivity; for example, captive
84 lions (*Panthera leo*) typically grow faster and achieve larger skulls than wild lions ²⁶. If
85 metabolic programming disruption occurs under captive conditions, where food
86 resources will differ from the wild, the potentially negative implications of this process
87 necessitate careful consideration in reintroduction programmes using captive-born or
88 reared animals. The same mechanism as apparent in laboratory animals and humans, if
89 present, in captive-born or reared animals released to the wild could compromise their

90 post-release health, survival, and reproductive success via altered metabolic rate and
91 associated increased body size, obesity and hyperphagia ²⁷.

92 To date, no studies have investigated the existence of metabolic programming in captive
93 endangered species. Here we address this knowledge gap by utilising a historically
94 collected dataset for the Iberian lynx (*Lynx pardinus*). Captive breeding and
95 reintroduction programmes are key components of the conservation action plan for this
96 species and have played an important role in improving its population status ²⁸ to the
97 point that it was recently downgraded from critically endangered to endangered on the
98 International Union for Conservation of Nature (IUCN) Red List ²⁹. Nonetheless, the
99 species remains the most endangered felid in the world and is restricted to habitats in
100 southern Spain and Portugal, where only two populations (Doñana and Sierra Morena)
101 remained prior to reintroduction efforts. These two populations had been isolated since
102 the 1950s ³⁰, with the smallest of these (Doñana) subsequently shown to be affected by
103 inbreeding depression ^{31,32}. Current conservation efforts are focused on the preservation
104 of the remnant populations, together with a reintroduction programme to recover the
105 species' historical distribution ³³.

106 A captive breeding programme for Iberian lynx was initiated in 2003, as part of the
107 conservation strategy for the species to ensure a healthy captive stock and eventually
108 provide individuals for release. The captive stock was initially founded with wild-
109 caught individuals that started breeding in 2004 ³⁴. The programme currently maintains
110 a high level of genetic variability in its captive population ³⁵ and these lynx are integral
111 to reintroduction efforts ³⁶. However, carnivore reintroduction programmes using
112 captive-bred animals are recognised as less successful than those using wild-sourced
113 individuals ^{37,38}. For Iberian lynx, the total confirmed mortality of released individuals
114 (regardless of age or duration since release) was 34% ³⁹, although earlier research

115 indicated mortality within the first 18 months of release was even higher (60%³⁷).
116 Importantly, captive-bred animals have a higher post-release mortality rate (52%) than
117 wild-born animals (29%)³⁶.

118 Our study explores the possibility that metabolic programming may be occurring within
119 the captive population of Iberian lynx. If so, this would represent a potentially
120 important, but overlooked, variable contributing to conservation outcomes. We tested
121 the ability of pre- and post-natal environment to predict energy intake or body weight
122 and whether an association existed between them. Specifically, we predicted that
123 captive-born and captive-reared individuals would express greater body size than wild
124 caught and wild-reared individuals as a function of energy intake.

125 **Results**

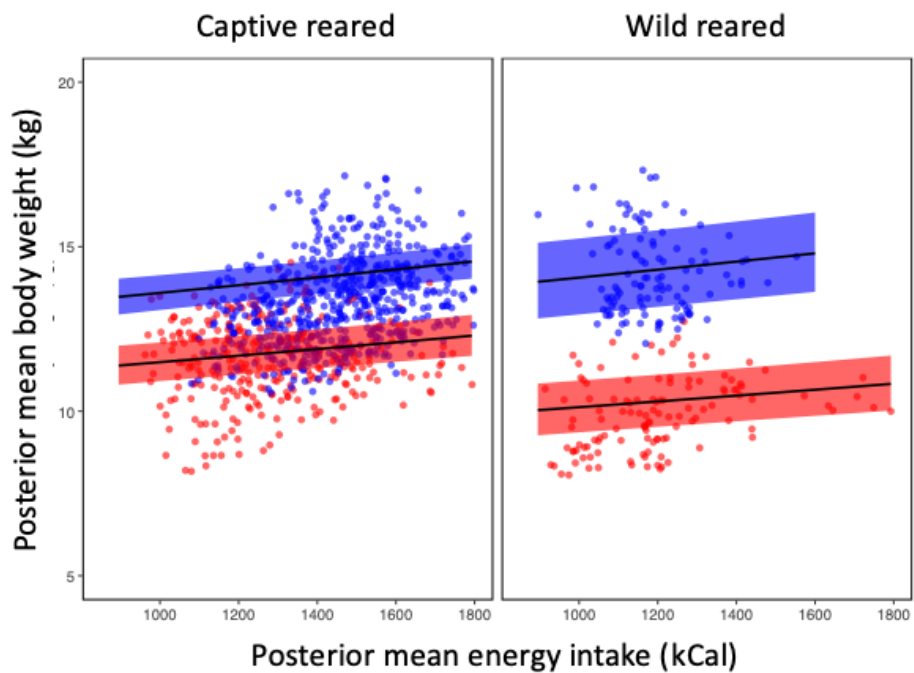
126 There was a statistically important interaction between sex and rearing environment on
127 lynx body weight (Table 1). Overall, males expressed a larger body weight than
128 females, irrespective of calorie intake (Fig. 1).

129

130 **Table 1.** Posterior mean estimates of body weight (kg) of Iberian lynx modelled using a
131 gamma GLMM with temporal dependency with individual fitted as a random term. CrI
132 is the 95% Bayesian credible interval. Credible intervals that do not contain zero
133 indicate statistical importance.

Model parameter	Posterior mean	Lower CrI	Upper CrI
Intercept	2.47	2.40	2.52

Sex _(male)	0.17	0.11	0.22
Rearing environment _(wild)	-0.13	-0.19	-0.06
Birth environment _(wild)	-0.07	-0.13	-0.01
Energy intake	0.02	0.01	0.03
Sex _(male) x Rearing environment _(wild)	0.16	0.07	0.25
Birth environment _(wild) x Energy intake	-0.02	-0.03	-0.01



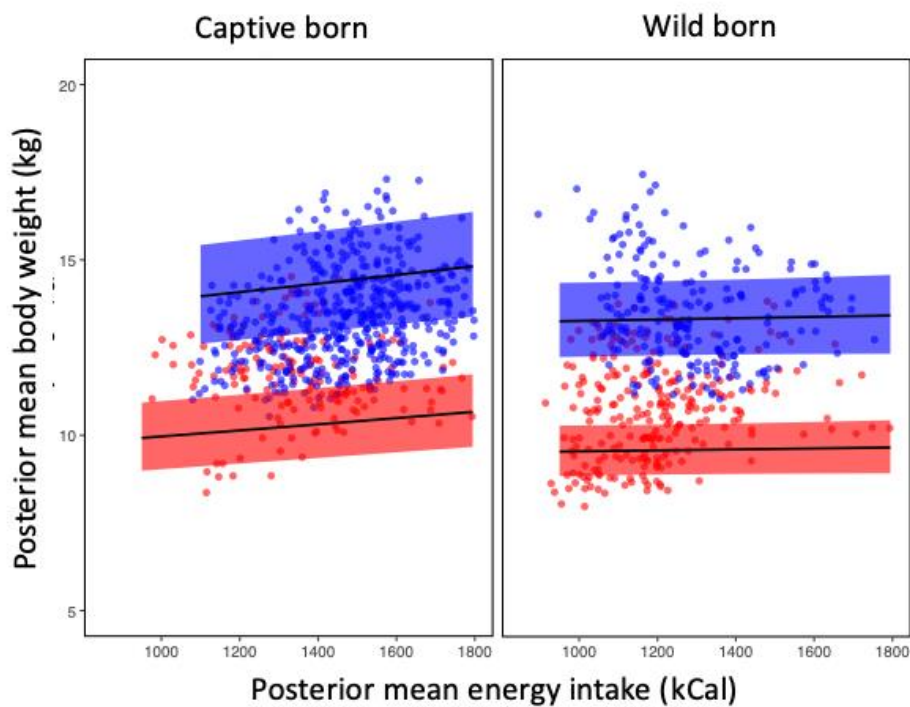
134

135 **Figure 1.** Posterior mean body weight (kg) of Iberian lynx, with 95% credible intervals
 136 (shaded area), as a function of mean daily energy intake (kCal) for male (blue) and

137 female (red) captive-reared and wild-reared individuals modelled with a Gamma
138 GLMM fitted with INLA.

139

140 This sex difference was more pronounced if animals were reared in the wild; females
141 were heavier when reared in captivity. Under the captive feeding regime (which
142 provided tailored food provisioning to individuals to ensure good body condition), there
143 was a statistically important interaction between birth environment and calorie intake on
144 body weight (Table 1). Captive-born individuals of both sexes showed a tendency to
145 gain weight as a function of calorie intake, while wild-born individuals did not (Fig. 2).



146

147 **Figure 2.** Posterior mean body weight (kg) of Iberian lynx, with 95% credible intervals
148 (shaded area), as a function of mean daily energy intake (kCal) for male (blue) and
149 female (red) captive-born and wild-born individuals modelled with a Gamma GLMM

150 fitted with INLA.

151

152 Female body weight did not predict the number of cubs produced by female lynx after
153 controlling for the number of litters produced (Table 2).

154

155 **Table 2.** Posterior mean estimates of number of kittens born to Iberian lynx modelled
156 using a negative binomial GLMM with individual fitted as a random term. CrI is the
157 95% Bayesian credible interval. Credible intervals that do not contain zero indicate
158 statistical importance.

Model parameter	Posterior mean	Lower CrI	Upper CrI
Intercept	-0.51	-2.14	0.88
Number of litters	0.59	0.29	0.95
Body weight	-0.01	-0.04	0.04

159

160 Lynx body weight as a function of height and length was not affected by age, or birth
161 and rearing environment (Table 3). Sex was statistically important in the model, with a
162 positive effect for males, indicating that even after adjusting for height and length,
163 males were heavier on average than females. There was a statistically important
164 interaction between height and length, indicating that larger-proportioned individuals
165 tended to be heavier than smaller-proportioned individuals (Table 3).

167 **Table 3.** Posterior mean estimates of body weight (kg) of Iberian lynx modelled using a
 168 gamma GLMM with individual fitted as a random term. CrI is the 95% Bayesian
 169 credible interval. Credible intervals that do not contain zero indicate statistical
 170 importance.

Model parameter	Posterior mean	Lower CrI	Upper CrI
Intercept	2.46	2.38	2.53
Sex _(male)	0.13	0.03	0.23
Rearing environment _(wild)	-0.01	-0.09	0.08
Birth environment _(wild)	0.01	-0.08	0.09
Age	0.02	-0.01	0.05
Height	0.03	-0.02	0.07
Length	0.07	0.03	0.12
Height x Length	-0.06	-0.09	-0.02

171

172 **Discussion**

173 Developmental programming leading to metabolic disorders is well recognised in
174 human medicine and has been demonstrated in laboratory studies of model animals
175 ^{1,3,4,6,40}. However, no previous studies have explored such disorders in the context of
176 captive breeding of an endangered species for the purpose of reintroduction.

177 Our results suggest a metabolic programming effect of pre- and post-natal environment
178 as reflected in birth and rearing conditions in the Iberian lynx. Three key findings were
179 evident from this study: a) captive-born lynx displayed a higher rate of energy intake
180 than wild-born individuals under a captive feeding regime tailored to ensure good body
181 condition; b) wild-born individuals maintained a stable body weight against energy
182 intake whereas captive-born individuals gained weight; and c) captive-reared females
183 achieved a larger body size than wild-reared females. None of these differences in body
184 weight and energy intake arose from changes in body proportions and we found no
185 evidence that female reproductive success in captivity was affected by body weight.

186 Captivity may demand lower activity levels ²⁵ in comparison with the natural
187 environment; the higher energy expenditure required in nature for foraging, predator
188 avoidance, reproduction, and other natural behaviours is effectively eliminated in
189 captivity ^{18,19}. It follows that captive animals tend to be larger than wild conspecifics,
190 attributed in some cases to the provision of larger rations in captivity ²⁵ and often
191 associated with obesity-related health concerns. Our captive wild-born lynx achieved
192 similar energy intakes to free-ranging conspecifics, i.e. a dietary intake of 1218 kcal
193 day⁻¹ (equating to one rabbit, approximately) for non-reproductive Iberian lynx ⁴¹.

194 Although a diet reflecting that of wild individuals is often considered an appropriate
195 benchmark for captive feeding, this feeding strategy may oversupply energy to captive-

196 born animals. Unlike their wild-born captive conspecifics, captive-born lynx in our
197 study had a higher daily energy intake (Figs 1 and 2) independent of their body size, and
198 exhibited weight gain in association with increased energy intake. Captive-born lynx
199 were previously reported to respond more quickly to changes in food provisioning
200 (either gaining or losing condition rapidly), thereby necessitating subsequent changes in
201 provisioning more often (J. Reeves, pers. obs.). Captive-born lynx were also observed to
202 more frequently consume their entire daily ration, whereas wild-born lynx were more
203 likely to leave uneaten food, particularly when meal size was increased in response to
204 body condition. This pattern of food intake is reflected by our analysis, which predicts a
205 greater caloric intake in captive-born animals in comparison with wild-born (Fig. 2).

206 Nonetheless, the larger body weights of captive-reared female lynx in our study
207 occurred in the absence of an effect of birth or rearing environment on body weight as a
208 function of height and length. Therefore, obesity did not explain these captivity-induced
209 changes in body weight, but rather body weight gain occurred alongside a proportional,
210 morphometric increase in size (Table 3). Although this finding may negate obesity
211 related health concerns, this captivity-induced phenotypic change may have
212 implications for conservation efforts that involve the release of captive-born individuals.

213 Additionally, the body condition of our study lynx were closely monitored (although not
214 recorded) and diet manipulated accordingly. As such, it is feasible that under a scenario
215 of less efficient dietary modification in response to observed body condition changes,
216 captive-born lynx may have been at risk of obesity. This outcome is particularly
217 important in light of the variable daily energy intake of lynx (1000-1800 kCal/day).

218 This variability reflects the rapid and frequent response of animal managers to changes
219 in lynx body condition. In this regard, wild-born lynx appeared to stabilise body
220 condition faster than captive-born animals and, therefore, required less frequent

221 adjustments to meal size (reflected in the lower credible intervals of the fitted model in
222 Fig. 2). However, disentangling the role of birth and rearing environment was not
223 possible in our data due to collinearity, such that all captive-born individuals were also
224 captive-reared.

225

226 In terms of weaned dietary provision, lynx in our study were exposed to consistent
227 dietary sources and species-appropriate feeding practices aligned with husbandry
228 guidelines ⁴², such that there is no reason to suspect that diet quality was limiting.
229 However, while dietary nutrient composition was not empirically determined it may
230 have affected growth ⁴³, while secondary or indirect nutritional factors may also have
231 been important. For example, rats can express an adaptive response when mothers are
232 overfed during pregnancy, with offspring programmed to high-fat diets through
233 increased food intake but not adiposity ²⁷. In other laboratory studies, high fat or low
234 protein gestational diets have been associated with phenotypic changes in the offspring
235 including obesity and a number of other metabolic disorders ².

236 A greater energy intake in captivity during the pre- and post-natal period could explain
237 the difference in body size of captive versus wild-reared females in our study. In
238 humans, females born to overweight mothers are taller and heavier than those born to
239 mothers with a normal weight, whereas patterns are less evident for males ²². In the
240 present study, sex differences were attributed to rearing environment and not birth
241 environment, providing evidence that post-natal feeding may play a key role in female
242 lynx growth. However, we could not determine if the differences in female body size
243 arose from maternal nutrition during lactation, or from food provisioning during the
244 post-weaning period; i.e. prior to cub independence from the mother at 6-8 months of
245 age ⁴⁴.

246 That captive-reared females were larger than wild-reared individuals, but with no
247 differences detected in males, may reflect the different energy requirements of the sexes
248 for development. Human mothers produce higher-energy breast milk for sons than for
249 daughters ⁴⁵. An adaptive explanation for this difference may be a higher growth rate in
250 males to enable them to attain a larger body size than females. Under this model of
251 maternal provisioning, together with competition among cubs for nipples ⁴⁶, high
252 maternal food provisioning in our study may have permitted a greater level of
253 nutritional assignment to female cubs than would naturally occur. Alternatively, male
254 cubs, which naturally require a higher energy intake, may have growth rates that are less
255 sensitive to maternal provisioning.

256 Diets that cause maternal obesity can lead to offspring resistance to leptin-signalling as
257 a result of exposure to high concentrations of leptin from maternal milk, resulting in
258 hyperphagia and consequent higher body weight ^{2,47}. This effect can derive from diets
259 fed during preconception, through pregnancy and lactation ^{2,48}. In our study, captive-
260 born lynx may have been programmed to a higher metabolic rate to take advantage of
261 high prey availability. In this regard, the relationship between body weight and energy
262 intake was most apparent (see slopes of Fig. 1 & 2) when the animals were evaluated
263 according to rearing conditions rather than birth conditions. It appears here that the post-
264 natal rearing phase (irrespective of rearing environment) may be more influential of
265 body weight than the pre-natal phase. This was particularly true for animals of wild-
266 origin, whereby those born in the wild (regardless of rearing environment) exhibited
267 little (if any) body weight change in response to increased energy intake, while those
268 born in the wild but also reared in the wild exhibited a positive relationship between
269 energy intake and body weight gain. This result suggests the potential for greater
270 metabolic sensitivity to energy intake in wild-reared animals, perhaps mediated through

271 reduced predictability or increased variability in daily intake experienced by free-
272 ranging animals. However, it is premature to suggest the observed response is adaptive
273 or whether pre- or post-natal rearing environment is a more influential predictor of final body
274 weight. Other variables, such as diet (including milk) composition, and maternal
275 breeding or rearing provenance, could account for the observed effects but could not be
276 tested here due to imbalance in the data. Likewise, paternal effects (reported in other
277 species ^{2,49,50}) could not be tested here but warrant further investigation.

278 Disruptions to metabolic programming also have the potential to alter phenotypes
279 through epigenetic effects across multiple generations ^{2,8,9,50,51}. Therefore, maladaptive
280 captive-born or -reared phenotypes have the potential to compromise the fitness not
281 only of the reintroduced individuals, but also of subsequent generations despite those
282 being born and reared in the wild. Longitudinal studies will hence be necessary to best
283 appreciate the extent and implications of this apparent developmental programming.

284 The implications of our findings for species conservation require consideration and
285 incorporation into future breeding and reintroduction programme planning. It has
286 already been shown that post-release mortality is higher in captive-bred animals than
287 wild-born animals ³⁶. Because lynx have smaller home ranges in areas with higher
288 densities of rabbits ^{52,53}, if reintroduced lynx are larger and have higher energy
289 requirements, this will likely translate into a requirement for a larger territory, or more
290 prey-dense habitat, in order to meet their elevated nutritional demands. Larger territories
291 would reduce lynx density in these areas, increasing the total area required to maintain a
292 viable population. Larger territories also increase the probability of encounters with
293 traffic and, thus, increase the possibility of mortalities from vehicle collisions, which is
294 already the major cause of death for released lynx ³³. Mortality rates of juveniles are
295 particularly high during the dispersal phase ⁵², and food availability is linked to the

296 successful settlement of juveniles ^{44,54}, hence individuals with increased dietary
297 requirements are under additional pressure. This is particularly concerning given that
298 low prey availability is already cited as a key cause of population declines, to the extent
299 that supplementary feeding has been implemented in some areas to support conservation
300 efforts ⁵⁴. The potentially greater supplementary food provisioning required to meet
301 increased nutritional requirements of captive-born released lynx has implications for
302 conservation resource investment. Moreover, the larger body size of captive-born
303 reintroduced individuals confers a competitive advantage in accessing higher quality
304 habitats such as those with higher prey density and/or feeding stations ⁵⁵ potentially
305 leading to the exclusion of smaller, wild-born animals.

306 A further conservation concern arises in relation to the potential impact of metabolic
307 programming on reproductive output, or survival to reproductive age. Although we
308 found no evidence for a change in reproductive success as a function of body size in
309 captive Iberian lynx (Table 2), no animals in our study suffered severe food restriction.
310 As such, the impact of the apparent metabolic programming detected in our study
311 population may not be realised until animals are released and subjected to variable prey
312 availability.

313 The potential health implications associated with a larger body size, or metabolic
314 disorders demonstrated in laboratory studies of other species ², may limit lifetime
315 reproductive potential via increased morbidity or mortality, or even intraspecific
316 competitive factors. Iberian lynx are a sexually dimorphic species, with body size the
317 main morphological difference between the sexes ⁵⁶. Territoriality in female mammals
318 has been explained through intra-sexual competition for food resources ⁵⁷ to cover the
319 higher energy requirements of females during gestation, lactation, and cub rearing. The
320 Iberian lynx is a solitary felid, with strong intra-sexual territoriality ⁵⁸. The larger body

321 size of captive-reared females could provide them a competitive advantage against
322 smaller, wild females which may be excluded from higher quality territories and
323 subsequent reproduction, thereby incurring indirect consequences for social
324 organisation within extant wild population and/or stimulating genetic bias towards
325 captive-reared phenotypes.

326 Alternatively, reproduction of released captive-reared females may be compromised if
327 females have higher nutritional needs for maintenance. Data on the energy requirements
328 for the weasel (*Mustela nivalis*), in which females are also smaller than males and males
329 do not participate in the rearing of the offspring, support the hypothesis that female
330 body size is limited by the elevated energy requirements of reproduction and cub
331 rearing⁵⁹. Reproductive success may also decline in response to limited food
332 availability as for the Canadian lynx (*Lynx canadensis*)⁶⁰, and larger females may be
333 more sensitive to minor changes in food availability than smaller females. Furthermore,
334 female Eurasian lynx (*Lynx lynx*) with cubs reduce their territory size during the first
335 weeks after birth⁶¹, such that protection of the litter may occur at the expense of
336 adequate prey acquisition.

337 In conclusion, to our knowledge this is the first study to demonstrate that the level of
338 feeding during pre- and post-natal development influences energy requirements in
339 adulthood for an endangered species. This study provides a vital first step in advancing
340 our understanding of metabolic development in felids and demonstrates that high levels
341 of feeding in captivity during pre- and post-natal development has implications for
342 metabolic programming of offspring and the sexually dimorphic trait of body size in the
343 Iberian lynx. Given that this species is listed as the most endangered of all felid species
344 and captive-bred animals play a key role in reintroduction efforts, such metabolic
345 programming raises concern for conservation and population recovery. Faced with a

346 mismatch between captive and wild food availability, post-release survival and
347 reproduction may be compromised in abnormally programmed captive-bred animals.
348 Whilst some studies have demonstrated a degree of reversibility in epigenetic effects ²,
349 it would appear prudent to aim for prevention, rather than treatment, of such
350 developmental programming, especially given the long-term and multi-generational
351 consequences. The negative effects of overfeeding may be mitigated with an appropriate
352 dietary intervention for breeding animals ⁵. Research is therefore warranted to further
353 investigate metabolic programming mechanisms and its effects in the Iberian lynx and
354 other taxa to inform and support the generation of evidence-based guidelines for captive
355 animal management.

356 **Methods**

357 **Study animals.** All data used in this study were obtained from El Acebuche Breeding
358 Centre (Doñana National Park, Matalascañas, Huelva, Spain). The captive population
359 initially comprised 26 wild-caught Iberian lynx that were brought into captivity as
360 founders between 2002 and 2008 ³⁴. The captive population subsequently increased in
361 size and now includes captive-born offspring as well as sporadic additions of
362 individuals from the wild which were either injured and could not be rehabilitated, or
363 imported for their genetic value ⁶². The dataset we examined comprised 22 animals (11
364 females, 11 males) that were included in the breeding stock for the centre between
365 23/03/2010 and 16/04/2017. The animals were categorised according to birth
366 environment as wild-born (n = 12) and captive-born (n = 10). Rearing environment was
367 similarly designated as either wild or captive; the cut-off point for classification of the
368 rearing period was at 54 days because the lynx weaning process occurs from 54 to 72
369 days old ⁶³. Wild-reared lynx (n = 7) were those that entered captivity older than 3
370 months of age, and captive-reared lynx (n = 15) were either born in captivity (n = 10; 7

371 mother-reared, 3 hand-reared), or entered captivity before the start of the weaning
372 process (n = 5; 2 needed hand-rearing, 3 were weaned when brought in).

373 Hand-rearing of cubs occurred occasionally when a cub's survival was considered
374 critical to the breeding programme. Hand-rearing was used for captive-born cubs when
375 mothers showed inefficient maternal care, abandoned their cub, or died. Wild-born cubs
376 have also been hand-reared, and consequently introduced into the captive breeding
377 programme due to the mother's death or improbability of survival in the wild. In these
378 cases cubs were bottle-fed with artificial milk until the age of 30 days when they were
379 offered small pieces of farmed European rabbit (*Oryctolagus cuniculus*) meat mixed
380 with milk. The European rabbit is the lynx's main prey ⁴¹ and its proportion in the
381 mixture was gradually increased until the cubs were eating only whole prey at an age of
382 approximately 100 days ⁶⁴. Starting between 9 and 12 months of age, lynx were fed 6
383 days week⁻¹ and fasted on the seventh day. The lynx's rations were reviewed weekly to
384 ensure good body condition; readjustments were made when lynx were observed to be
385 over-weight or under-weight, according to the body condition standards ⁶⁵. This
386 assessment included a visual (and when possible, palpable) assessment of the animal's
387 body fat and aligned with published body condition scoring systems for felids ^{66,67}. This
388 feeding adjustment protocol was applied comparably among individuals regardless of
389 birth or rearing origin, and the frequency or extent of adjustments to ration were decided
390 on the basis of animal condition and response to food provisioning.

391 **Data collection.** As part of the management system of El Acebuche Breeding Centre,
392 individual husbandry records are maintained for each lynx, including daily feed intake
393 recorded to the nearest gram, calculated as amount offered less uneaten remains. In
394 accordance with wild lynx dietary intake ⁶⁸, animals were primarily fed farmed
395 European rabbit, as whole or dressed carcasses. Lynx were also fed chicken breast, beef,

396 whole quail (*Coturnix coturnix*) and whole partridge (*Alectoris rufa*). The total
397 metabolisable energy content of the diet (ME; kcal) was calculated using Atwater
398 factors for each food type and the quantity of each consumed per month. The Atwater
399 factors used for beef, chicken breast, and rabbit muscle meat were unmodified (i.e. $4 \times$
400 crude protein (CP), $9 \times$ crude fat (CF), and $4 \times$ nitrogen-free extract (NFE)), as
401 recommended for raw foods ⁶⁹, whilst modified Atwater factors (i.e. $3.5 \times$ CP, $8.5 \times$ CF,
402 and $3.5 \times$ NFE) were used for feed items with predicted lower digestibility (i.e. whole
403 prey; quail, partridge, rabbit, and chicken) ⁷⁰. The nutrient composition of each dietary
404 component was determined from the published literature (beef, chicken muscle meat,
405 rabbit muscle meat, and quail carcass ⁷¹; partridge, dressed rabbit carcass, and whole
406 chicken ⁷²; and previously published data used for chicken and beef bone ⁷³; whole
407 rabbit ⁷⁴; and rabbit meat with bone ⁷⁵). Total energy contribution was subsequently
408 calculated based on the proportional contribution of each food type to the consumed
409 meal. The mean daily energy intake of each individual was calculated for the 30 days
410 prior to each weighing data point.

411 Body weight ($\text{kg} \pm 0.1$) data were obtained during periodic routine husbandry checks.
412 Animals were weighed prior to feeding on an opportunistic or routine basis (typically
413 every 1-3 months). Individual body height and length measurements (cm) were obtained
414 during veterinary examination under general anaesthesia. Body height was measured as
415 the distance from the metacarpal pad to the shoulder, and body length as the distance
416 from the tip of the nose to the base of the tail following the body shape ⁶⁵, as per
417 methods used in other species ⁷⁶⁻⁷⁸.

418 Data were only used from lynx that were fed individually and observed daily, to ensure
419 certainty of the quantity of food ingested. Similarly, data during periods of gestation,
420 lactation and cub growth until 2 years of age were excluded because monitoring

421 individually ingested quantities of food is imprecise during these periods due to
422 husbandry protocols preventing close contact with the animals. The dataset comprised
423 1160 records, with details of individual birth environment (wild, captive), rearing
424 environment (wild, captive), body weight, and estimated daily energy intake. Age data
425 were calculated from birth date which was accurate to the day (for captive-born
426 individuals) or month (± 1 month for wild-born individuals; estimated on the basis that
427 lynx have one breeding season per year and births occur within a two-month period
428 each year). Wild-born lynx entered captivity either as cubs, or as adults which had been
429 monitored since birth and, therefore, year of birth was known for all of them. Cubs
430 obtained during the birthing season had day of birth estimated on the basis of
431 developmental stage (e.g. eye and ear flap opening, dental eruptions). To investigate
432 potential impact on reproductive success, data for the total cumulative number of litters
433 and cubs surviving until 2018 produced by each female were used as a proxy for
434 reproductive success. An additional subset of data (55 records) comprised body height,
435 length and weight, measured at irregular intervals, for every individual.

436 **Data analysis.** To make inferences about model parameters a Bayesian approach was
437 used. Bayesian inference is robust in dealing with unbalanced data, dependency due to
438 repeated measures, and a non-normal response variable. This approach also avoids
439 reliance on hypothesis testing and P-values, which are increasingly recognised as
440 unreliable statistical tools for any but the simplest models ⁷⁹⁻⁸¹.

441 Data were modelled using R version 3.5.2 ⁸² with models fitted in a Bayesian
442 framework using integrated nested Laplace approximation (R-INLA) ⁸³. To
443 accommodate temporal dependency in the data, body weight was modelled using a
444 random walk (RW1) trend model fitted for age following a gamma distribution, which
445 assumed body weight was strictly positive and continuous. All measured variables were

446 included in an initial model with an optimal fixed structure identified with a backward
 447 selection procedure based on Watanabe-Akaike Information Criterion (WAIC) ⁸⁴. To
 448 assess final model sensitivity to priors, we re-ran models with PC and half-Cauchy prior
 449 distributions on hyperparameters, which yielded qualitatively identical outcomes in all
 450 cases (results not shown).

451 The best-fitting model for lynx body weight, identified by backward selection, was:

$$452 \quad Wt_{ijk} \sim \text{Gamma}(\mu_{ijk}, \phi)$$

$$453 \quad E(Wt_{ijk}) = \mu_{ijk} \text{ and } \text{var}(Wt_{ijk}) = \frac{\mu_{ijk}^2}{\phi}$$

$$454 \quad \log(\mu_{ijk}) = \eta_{ijk}$$

$$455 \quad \eta_{ijk} = \beta_1 + \beta_2 \times \text{Sex}_{ijk} \times \beta_3 \times \text{Rear}_{ijk} + \beta_4 \times \text{Birth}_{ijk} \times \beta_5 \times \text{kcal}_{ijk} + \text{lynx}_j$$

$$456 \quad + \text{age}_k$$

$$457 \quad \text{lynx}_j \sim N(0, \sigma_{\text{lynx}}^2)$$

$$458 \quad \text{age}_k \sim N(0, \sigma_{\text{age}}^2)$$

459 Where Wt_{ijk} is the body weight on day i for lynx j at age (age) k , which assumes body
 460 weight follows a gamma distribution with mean μ and precision ϕ . Sex_{ijk} is a categorical
 461 covariate corresponding with sex, male and female. The variables Birth_{ijk} and Rear_{ijk} are
 462 also categorical covariates, each with two levels, corresponding with birth (wild,
 463 captive), and rearing provenance (wild, captive). The variable kcal_{ijk} , is a continuous
 464 covariate corresponding with daily estimated kilocalories consumed by an individual
 465 lynx during the 30 days prior to weight measurement. The random intercept lynx_j was
 466 included to introduce a correlation structure between weight measurements for the same
 467 individual, with variance σ_{lynx} distributed normally and equal to 0.

468 Data were also fitted to a model for the total number of cubs produced by each female,
 469 which took the form:

$$470 \quad \text{Cubs}_i \sim \text{NB}(\mu_i, k)$$

$$471 \quad E(\text{Cubs}_i) = \mu_i \text{ and } \text{var}(\text{Cubs}_i) = \mu_i + \frac{\mu_i^2}{k}$$

$$472 \quad \log(\mu_i) = \eta_i$$

$$473 \quad \eta_i = \beta_1 + \beta_2 \times \text{Wt}_i + \beta_3 \times \text{Litter}_i$$

474 Where Cubs_i is the number of offspring produced by female lynx i assuming a negative
 475 binomial distribution with mean μ and dispersion k . The variables Wt_i and Litter_i are
 476 continuous covariates corresponding with lynx body weight (kg) and total number of
 477 litters, respectively.

478 Lynx body weight was modelled using height and length data to examine whether body
 479 proportions, along with sex, birth and rearing provenance influenced body size.

480 The model took the form:

$$481 \quad \text{Wt}_{ij} \sim \text{Gamma}(\mu_{ij}, \phi)$$

$$482 \quad E(\text{Wt}_{ij}) = \mu_{ij} \text{ and } \text{var}(\text{Wt}_{ij}) = \frac{\mu_{ij}^2}{\phi}$$

$$483 \quad \log(\mu_{ij}) = \eta_{ij}$$

$$484 \quad \eta_{ij} = \beta_1 + \beta_2 \times \text{Sex}_{ij} + \beta_3 \times \text{Rear}_{ij} + \beta_4 \times \text{Birth}_{ij} + \beta_5 \times \text{age}_{ij} +$$

$$485 \quad \beta_6 \times \text{height}_{ij} + \beta_7 \times \text{length}_{ij} + \text{lynx}_j$$

$$486 \quad \text{lynx}_j \sim N(0, \sigma_{\text{lynx}}^2)$$

487 Where age_{ij} was lynx age on day i for lynx j , assuming body weight ($W_{t_{ij}}$) follows a
488 gamma distribution with mean μ and precision ϕ . The variables $height_{ij}$ and $length_{ij}$ were
489 continuous covariates corresponding with body height and length respectively.
490 Individual lynx ($lynx_j$) were included as a random term in the model.

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499 **Data Availability**

500 The full dataset used in this study is available on request from the Organismo
501 Autónomo Parques Nacionales (Ministerio para la transición ecológica y el Reto
502 Demográfico) at: buzon-direccion@oapn.es.

503 **Author contributions**

504 J.R., E.S.D., and K.W-T. conceived the study and designed it with assistance from C.S.
505 J.R. collated data for statistical analyses; C.S. completed all data analyses. Interpretation
506 was conducted by all authors.
507 J.R. and K.W-T. prepared and wrote the manuscript with input from all authors.
508 The authors declare no competing interests.

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