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1 Computed tomography reveals hip
2 dysplasia in *Smilodon*:
3 Implications for social behavior in an
4 extinct Pleistocene predator
5

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25 **Abstract**

26 Reconstructing the behavior of extinct species is challenging, particularly for
27 those with no living analogues. However, damage preserved as paleopathologies on
28 bone can record how an animal moved in life, potentially reflecting patterns of behavior.
29 Here, for the first time, we use computed tomography (CT) to assess hypothesized
30 etiologies of pathology in a pelvis and associated right femur of an adult *Smilodon*
31 *fatalis* saber-toothed cat, one of the best-studied mammal species from the Pleistocene-
32 age Rancho La Brea asphalt seeps, Los Angeles, California. The pelvis exhibits
33 massive destruction of the right acetabulum that previously was interpreted, for nearly a
34 century, to have resulted from trauma and infection. We evaluated this historical
35 interpretation using CT imaging to supplement gross morphology in identifying
36 symptoms of traumatic, infective, or degenerative arthritis. We found that the pathologic
37 distortions are inconsistent with degenerative changes that started only later in life, as in
38 the case of infective or traumatic arthritis. Rather, they characterize chronic remodeling
39 that began at birth and led to degeneration of the joint over time. These findings suggest
40 that this individual suffered from hip dysplasia, a congenital condition common in
41 domestic dogs and cats.

42 The individual examined in this study reached adulthood (at least four to seven
43 years of age) but never could have hunted properly nor defended territory on its own. As
44 such, this individual, and other critically pathologic *Smilodon* like it, likely survived to
45 adulthood by association with a social group that assisted it with feeding and protection.
46 The pathologic specimens examined here in detail are consistent with a spectrum of
47 social strategies in *Smilodon* supported by a predominance of previous studies. This

48 application of a relatively new and interdisciplinary technique to an old question
49 therefore informs the longstanding debate between social and solitary hypotheses for
50 the behavior of an extinct predator.

51

52 **Introduction**

53 The saber-toothed cat *Smilodon fatalis* is one of the most well-studied apex
54 predators from the late Pleistocene epoch, if not across the entire history of fossil
55 mammals [1]. Much of our knowledge about this species comes from the Rancho La
56 Brea asphalt seeps in Los Angeles, California, United States, which selectively trapped
57 and preserved thousands of individuals of *Smilodon* from at least 50,000 years ago until
58 the species' extinction approximately 11,000 years ago [1]. The seeps functioned as a
59 carnivore trap: a large herbivore stuck in the asphalt inadvertently would attract large
60 carnivores and scavengers, which themselves would become entrapped in great
61 numbers [2]. Studies of *Smilodon* at Rancho La Brea have enabled reconstruction of its
62 feeding behavior as an ambush predator specializing on herbivorous megafauna,
63 inferences derived using independent approaches ranging from comparative
64 morphology (e.g. [3]) to stable isotopes (e.g. [4]). As well, the abundant specimens
65 include numerous examples of healed injuries, or pathologies [5]. Paleopathologies
66 preserved as skeletal lesions are a phenomenon that tends to be rare at more typical
67 fossil sites that do not involve preservation in asphalt, do not exhibit a carnivore bias, or
68 generally have undergone different taphonomic processes; but this phenomenon is
69 captured by Rancho La Brea's large sample sizes.

70 As bone remodels throughout an animal's life in response to stress, strain, and
71 injury [6–9], paleopathologies can preserve a record of realized behavior and
72 supplement the picture of potential behavior presented by skeletal morphology.
73 Differences in the distribution of pathologies throughout the skeleton, for example,
74 distinguish *Smilodon* from a contemporaneous predator, the dire wolf *Canis dirus*,
75 reflecting differences between the two species in hunting behavior and potential prey
76 preference corroborated by independently gathered data (e.g. [4]). While injuries in dire
77 wolves tended to be concentrated around its distal limbs, supporting the hypothesis that
78 it was a pursuit predator, *Smilodon's* injuries tended to cluster around the midline of its
79 body, supporting inferences that it ambushed and grappled with prey [5]. As the
80 aggregate result of how an animal moved over the course of its life, pathologies present
81 a relatively direct record of the animal's interactions with its prey, its environment, and
82 even its conspecifics—including, potentially, intraspecific interactions such as agonistic
83 behavior and sociality.

84 Sociality, the degree to which individuals live with conspecifics in groups or
85 societies [10], is difficult to infer in *Smilodon* given that it has no direct living analogues.
86 Estimated to have weighed between 160 and 350 kg [3,11], *Smilodon* was at least the
87 size of the Siberian tiger (*Panthera tigris altaica*), the largest extant felid; some
88 estimates reach 369 to 469 kg, placing *Smilodon* in the range of the largest extant
89 ursids [12,13]. No felid living today has *Smilodon's* elongate, knife-like canines or stocky
90 and powerful build. As well, *Smilodon* (of the extinct felid lineage Machairodontinae) is
91 distantly related to extant large felids (Felinae), introducing further uncertainty. Based
92 on its robust morphology (e.g. [14,15]) and on evidence from stable isotopes (e.g. [4]), it

93 likely stalked and ambushed its prey; therefore, it may have been similar to the African
94 lion (*Panthera leo*), which has a similar hunting strategy and is social [16]. Yet sociality
95 varies across mammalian species, including among members of a single genus; other
96 extant pantherines like tigers (*Panthera tigris*) are solitary [17], complicating inferences
97 of behavior based on ancestral reconstructions. Advocates of the solitary-cat hypothesis
98 cite *Smilodon*'s small relative brain size determined using endocranial casts [18] as
99 evidence of solitary behavior, because sociality exerts high cognitive demands [19,20].
100 However, compared to ungulates and primates, carnivores have tended to decouple
101 sociality and relative brain size, so that a smaller braincase does not necessitate a lack
102 of sociality [21]. The gregarious-cat hypothesis has drawn support from the high ratios
103 of *Smilodon* relative to prey at Rancho La Brea [14,22,23] (although detractors point out
104 that some extant large cats aggregate at kills and carcasses despite otherwise being
105 solitary [20]) and from comparisons between Rancho La Brea and playback
106 experiments used to estimate carnivore abundance in Africa, which suggest that the
107 densities of *Smilodon* at Rancho La Brea are more consistent with it having been social
108 rather than solitary [24,25]. The lack of size sexual dimorphism in *Smilodon* relative to
109 living or fossil lions has supported monogamy rather than polygynous breeding in
110 *Smilodon*, if the saber-tooth did have a social structure [26]. Most relevant to the current
111 study, the existence of healed injuries in *Smilodon* also has been interpreted as
112 evidence for social behavior, with the assumption that recovering from serious injury
113 would be difficult if not impossible without cooperative sociality [27].

114 The current study centers on a *Smilodon* specimen (LACMHC 131) that has
115 earned the distinction of being “the most strikingly pathological object in the collection of

116 Rancho La Brea fossils” [22]. The specimen is a right innominate bone exhibiting
117 massive distortion and destruction of the hip socket (Figure 1). Moodie [22], restricted in
118 1930 to an inspection of the gross morphology, regarded this specimen as having been
119 infected following violent trauma, possibly during an encounter with a conspecific, which
120 also led to dislocation of the femur from the hip. Moodie found no pathologic bones
121 potentially associated with the injured innominate; because of disarticulation by flowing
122 asphalt over thousands of years, associated elements are rarely encountered at
123 Rancho La Brea. However, after over half a century, Shermis [23] described a
124 pathologic femur (LACMHC 6963; Figure 2) associated with another pathologic pelvis.
125 Later, this femur was determined to be associated instead with the Moodie specimen
126 [27], enabling examination of the effects of a single injury on associated skeletal
127 elements using newer technology.

128 **Fig 1.** Photographs of LACMHC 131, a pathologic pelvis belonging to *Smilodon*
129 *fatalis*. **(A)** Lateral view of right side showing destruction of the acetabulum;
130 anterodorsal end to the right. **(B)** Lateral view of left side showing the intact acetabulum
131 but exostoses around the anterodorsal acetabular rim; anterodorsal end to the left. **(C)**
132 Dorsal and **(D)** ventral views showing asymmetry in the pelvis; anterior end to the right.

133 **Fig 2.** Photographs of LACMHC 6963, a pathologic right femur belonging to
134 *Smilodon fatalis*. **(A)** Anterior and **(B)** posterior views of full femur, excluding the distal
135 epiphysis, which was broken after death; proximal end on the left. **(C)** Anterior and **(D)**
136 posterior close-up views of the proximal end. **(E)** Dorsal close-up view of the femoral
137 head, greater trochanter, and lesser trochanter in lower center background. **(F)** Lateral
138 close-up view of the greater trochanter and lesser trochanter (lower center), which is

139 enlarged into a round knob. The upper scale bar refers to A and B and the lower scale
140 bar refers to C, D, E, and F.

141 In the present study, we supplement gross morphology and analyze LACMHC
142 131 and 6963 using computed tomography, observing, for the first time, the internal
143 bone structure of a pathologic non-primate mammal. We evaluate the historical
144 inference that the injury was the result of trauma and assess different etiologies of
145 pathology: traumatic arthritis, infective arthritis, or degenerative arthritis. Finally, we
146 explore the implications of the diagnosis on reconstructions of sociality in *Smilodon* and
147 the potential contribution of paleopathology to a growing interdisciplinary body of
148 literature supporting sociality in this extinct predator.

149

150 **Materials and Methods**

151 All specimens examined are from the collections of the La Brea Tar Pits and
152 Museum, part of the Los Angeles County Natural History Museum (LACM), Los
153 Angeles, California. Different fossiliferous asphaltic deposits (which became manmade
154 “pits” during the historical excavation process) at Rancho La Brea had different periods
155 of asphalt seep activity, thus entrapping organisms over different timespans over the
156 past 55,000 years with varied depositional environments and taphonomic histories. In
157 this context, we reduced potential variability in these factors by selecting all specimens
158 from a single deposit, Pit 61/67. Pit 61/67 is the most recent deposit at Rancho La Brea
159 that precedes the late Pleistocene megafaunal extinctions at around 11,000 years
160 before present [28], at which point *Smilodon fatalis* became extinct.

161 We examined the external surfaces of the pathologic pelvis including the right
162 innominate (LACMHC 131) and associated pathologic right femur (LACMHC 6963). As
163 specimens for comparison, we inspected an unassociated non-pathologic right femur
164 (LACMHC K-3232) and a non-pathologic pelvis (LACMHC K-2584) from the same
165 deposit and of similar sizes and ontogenetic stages as the pathologic specimens. Initial
166 surface scanning of all specimens was carried out using an Artec Space Spider (Artec
167 3D) as a means of digital preservation and to provide a 3D visual with color. The
168 surface scans were processed in Artec Studio 12 and fused into a model with a
169 resolution of 0.2 mm. CT imaging of LACMHC 131, 6963, and K-3232 was performed at
170 the S. Mark Taper Foundation Imaging Center, Los Angeles, California, on a GE
171 Revolution (GE Healthcare, Waukesha, WI) 256-slice scanner with 0.625 mm slice
172 thickness. Imaging parameters were KVP=120, mA=300, 0.5 second rotation time, and
173 0.51 pitch using a medium body FOV. The data were acquired in the axial plane,
174 reformatted into soft tissue and bone algorithms, and viewed in the axial, coronal and
175 sagittal planes. CT images were converted to 3D models using the segmentation
176 software Mimics (Materialise). Geomagic Freeform (3D Systems) was used to upload
177 and determine placement of the plane for cross-sections of the 3D reconstructions.

178 No permits were required for the described study, which complied with all
179 relevant regulations.

180

181 **Results**

182 LACMHC 131 is a pathologic but complete pelvis with all sutures completely
183 fused (Figure 1; File S1; Movie S1). The distal end of LACMHC 6963, the pathologic
184 femur, is broken and missing (Figure 2; File S1), precluding verification of distal
185 epiphyseal fusion. However, the proximal epiphyses are completely fused to the shaft,
186 and the size of the femur is comparable to large adult femora belonging to other
187 *Smilodon* preserved at Rancho La Brea. Therefore, the *Smilodon* individual represented
188 by these two specimens is inferred to have been of adult age.

189 There are no signs of callus, or bone regeneration and healing, that typically are
190 seen on imaging following fracture. Rather, the osteophytes are likely a sign of bone
191 remodeling secondary to malformation of the joint with subsequent necrosis. The
192 changes in the right acetabulum and right femur are consistent with those expected
193 from repetitive subluxation and subsequent necrosis. The right acetabulum is shallow
194 and elliptical-shaped as opposed to concentric-shaped. A hole in the bone, likely the
195 result of posthumous asphaltic wear based on its sharp edges, marks the thin medial
196 wall of the acetabulum, which is lined otherwise with exostoses. The left acetabulum
197 appears non-pathologic; however, the ilium anterodorsal to the acetabulum—origin of
198 the quadriceps femoris muscles—bears rugose ridges (Figure 1; File S1, Movie S1)
199 absent on typical *Smilodon* pelvic specimens (Figure 3). The head of the pathologic
200 right femur is flattened and laden with anatomical distortions; as well, the lesser
201 trochanter is enlarged into a round knob (Figure 2; File S1). The non-pathologic right
202 femur, the comparative specimen, bears a round head that is appropriately developed
203 (Figure 4), fitting snugly into a concentric-shaped socket such as the left acetabulum of

204 the pathologic pelvis or either acetabulum of the non-pathologic pelvis (Figure 3) and
205 thereby allowing for an axis of rotation and movement expected for *Smilodon* to function
206 normally.

207 **Fig 3.** Photographs of LACMHC K-2584, a non-pathologic pelvis belonging to
208 *Smilodon fatalis*. **(A)** Lateral view of right side; anterodorsal end to the right. **(B)** Lateral
209 view of left side; anterodorsal end to the left. **(C)** Dorsal and **(D)** ventral views; anterior
210 end to the right.

211 **Fig 4.** Photographs of LACMHC K-3232, a non-pathologic right femur belonging
212 to *Smilodon fatalis*. **(A)** Anterior and **(B)** posterior views of full femur; proximal end on
213 the left. **(C)** Anterior and **(D)** posterior close-up views of the proximal end, including the
214 spherical femoral head, greater trochanter, and lesser trochanter. **(E)** Dorsal close-up
215 view of the femoral head, greater trochanter, and lesser trochanter in lower center
216 background. **(F)** Lateral close-up view of the greater trochanter and lesser trochanter
217 (lower center). The upper scale bar refers to A and B and the lower scale bar refers to
218 C, D, E, and F.

219 The four cardinal findings of arthritis on imaging are bony sclerosis, osteophytes,
220 joint space narrowing, and subchondral cysts. The CT images of the pathologic
221 specimens reveal evidence of degenerative changes in the right hip joint and a lack of
222 fractures from traumatic impact (Movie S2; Datasets S1-S3). The images demonstrate
223 findings of sclerosis and osteophytes in both the right acetabulum and femoral head,
224 which are changes consistent with degenerative arthritis. Profuse remodeling with
225 osteophyte formation marks the right femoral head, likely in response to the
226 degenerative process from repeated subluxation and dysplasia.

227

228 **Discussion**

229 **Diagnosis**

230 The arthritic degeneration seen in the pathologic specimens and visualized on
231 CT imaging must have arisen from one of three etiologies: traumatic arthritis, infective
232 arthritis, or degenerative arthritis. Findings on the specimens make the etiologies of
233 infective arthritis or traumatic arthritis less likely. In the case of infective arthritis, the
234 presupposition is that the specimen developed typically before an insult that led to
235 infection and subsequent obliteration of the hip joint. This assumption also holds true for
236 the case of a traumatic arthritis etiology following an injury or fracture.

237 However, the anatomical distortions of the right femoral head, in conjunction with
238 the obliteration of the right acetabulum seen in the gross specimens as well as on CT
239 imaging, suggest chronic changes that led to degeneration over time (Figure 2). The
240 degeneration of the head of the femur as seen would not be expected if the etiology of
241 degenerative change in the hip joint were due to infection or trauma, as the
242 development of the pelvis and femur presumably would have been complete before the
243 insult or injury occurred during the adult cat's life.

244 Instead, the condition of the right acetabulum and right femoral head
245 demonstrates anatomy consistent with developmental distortion. Typically, the head of
246 the femur develops in conjunction with the acetabulum of the pelvis [29]. The spherical
247 femoral head fits into the concentric-shaped acetabulum to form a ball-and-socket joint
248 that enables a four-legged creature to ambulate normally, lie down, sit down, stand up,

249 and function without subluxation, or displacement, of the femoral head out of the pelvic
250 socket [29]. In developmental hip dysplasia, however, the acetabulum of the pelvis does
251 not develop appropriately, which subsequently affects the development of the head of
252 the femur [29]. An elliptical acetabulum, as opposed to concentric-shaped, causes
253 continual subluxation of the femoral head, which can result in coxa plana, or necrosis of
254 the bony nucleus of the femoral head. This subsequent coxa plana produces flattening
255 and degeneration of the normally spherical femoral head [30].

256 Proper anatomical development and ossification of the hip joint rely on
257 continuous and symmetrical pressure of the femoral head on the acetabulum, and
258 dysplasia results from improper positioning of the femoral head within the acetabulum
259 [29,31]. Dysplastic hips are characterized by a pathologic restructuring of the hip and
260 accelerated remodeling of the joint in response to abnormal forces and tensions that
261 create stress. This produces formation of new bone in some areas and resorption of
262 bone in others, ultimately causing degenerative joint disease [29].

263 This pathology starts to impact movement at the time of first walking, although
264 minimal pain would ensue because of the animal's flexibility at its early age. As the joint
265 cartilage wears out, however, bone would rub on bone. The ensuing forces would make
266 the bone stiffer, resulting in osteophytes or bone spurs as well as sclerosis that
267 manifests on CT imaging as increased bone density (Movie S2; Datasets S1-S2). At this
268 point, loading the limb would cause pain, and range of motion would be limited.
269 Therefore, the animal examined in this study would have spent as little time as possible
270 on its right hind leg, needing to compensate for the handicap by increasing the load on
271 its left hind leg. This compensation would explain the exostoses on the left ilium

272 anterodorsal to the otherwise non-pathologic acetabulum (Figure 1; File S1; Movie S1),
273 indicating abnormal pulling of the quadriceps femoris muscles originating in this area.

274 **Hip dysplasia in modern carnivorans**

275 Hip dysplasia is a heritable, polygenic condition that can affect a range of
276 mammal species [29], including humans [32–34]. Feline hip dysplasia is reported
277 clinically relatively rarely [35,36], but canine hip dysplasia (CHD) is one of the most
278 prevalent orthopedic diseases in domestic dogs [37] and, since it is similar to
279 developmental dysplasia of the human hip [38], is very well studied.

280 Embryologically, articular joints differentiate from skeletal mesenchyme *in situ*
281 with the support of surrounding tissues that sustain mechanical and physiological forces
282 that tend to pull on the joints [29,39]. Dog hip joints are normal at birth, as teratologic
283 factors and the mechanical stresses that could displace the femoral head are rare at
284 this time [29]. In humans, fetus positioning—particularly the legs in adduction and
285 extension—contributes to the development of hip dysplasia; the congruity of the
286 acetabulum and femoral head is not maintained, making joint laxity more likely [29].
287 Additionally, suboptimal muscle function may be a major contributor to joint laxity, which
288 in turn has been postulated to be a major contributor to the characteristic acetabular
289 and femoral changes observed in hip dysplasia [29].

290 Epiphyseal ossification normally begins by 12 days of age in canines. In canines
291 that eventually develop CHD, anatomical changes of the femoral head and pelvic socket
292 begin prior to week three of development [40]. In dysplastic hips, the teres ligament,
293 which is crucial for holding the femoral head in place, is too short; this produces
294 luxation, or dislocation, of the top of the femoral head, beginning at around seven weeks

295 of age [29]. This luxation increases throughout development, degrading the articular
296 cartilage that surrounds the femoral head and delaying ossification of the femur and
297 acetabulum [29]. Dysplasia also results in shortening of the affected limb, as the femoral
298 head is positioned higher in the acetabulum.

299 The overall results of these physiologic changes are mechanical imbalance and
300 instability in the hip joint causing displacement due to opposing forces from the
301 acetabulum and femoral head, and osteophytes in the acetabulum to compensate for
302 cartilage loss [29].

303 **Hip dysplasia and osteoarthritis in domestic and wild cats**

304 Feline hip dysplasia (FHD) often is not detected clinically in domestic cats
305 [36,41], possibly because it does not commonly cause overt functional impairment or
306 because cats are able to compensate for the resulting lameness better than dogs
307 [42,43]. As a result, much fewer clinical cases of FHD are reported [35,36] in contrast to
308 cases of CHD [37]. In these cases, osteoarthritis (also known as degenerative joint
309 disease, or DJD) of the hip secondary to FHD is well known [44]. Osteoarthritis was
310 recorded in 43 of 45 (95.6%) of cats with FHD [45]. As well, in 5 of 13 (38.5%) cases of
311 hip osteoarthritis with an identifiable radiographic or historical cause, hip dysplasia was
312 pinpointed as the cause, with the remaining cases resulting from trauma or equivocal
313 between trauma and dysplasia [42].

314 Reports of FHD in non-domestic large cats are even rarer than in domestic cats.
315 Snow leopards in zoologic institutions have exhibited hip dysplasia; across 14 zoos,
316 seven cases were classified as moderate to severe [46,47]. At least two individual snow
317 leopards necessitated total hip replacement before being able to breed [46,47]. Beyond

318 snow leopards, accounts of functional impairment in the hip of non-domestic large cats
319 tend to report osteoarthritis, which can be associated with FHD but may also stem from
320 trauma and increased age [48–50].

321 For wild-caught large cats, the only comprehensive study of which we are aware
322 is a survey of 386 individuals (283 wild-caught) across three felid genera mounted as
323 exhibit skeletons in a range of North American natural history museums [49]. Though
324 not focusing specifically on hip dysplasia, the study tracked DJD, which may be
325 associated with hip dysplasia [42,45]. The sample recorded DJD in 9.7% of 31 tigers,
326 2.3% of 88 African lions, and 5.1% of 59 mountain lions, and none in five other species
327 of big cat. These frequencies are low compared to domestic cats, perhaps owing to
328 differences in body size, diet, and lifestyle between large wild cats and domestic cats
329 [44]. Though this study identified instances of non-inflammatory osteoarthritis in the
330 shoulder, elbow, and stifle, it found none in the hip. However, 4% of all joints afflicted by
331 spondyloarthropathy—a form of inflammatory arthritis—comprised the hip [49].

332 **Behavioral implications for *Smilodon***

333 Previous workers have inferred social behavior from *Smilodon's* pathologies,
334 interpreting signs of healing as evidence that the animal continued to live after injury.
335 Given the severity of many of the injuries, authors argue, the animal would have starved
336 to death had it not lived within a social structure. The fact that the present pathology
337 would have manifested from a young age, hindering the animal's ability to hunt prey and
338 defend territory over the course of its life, is even more indicative of social structure.

339 *Smilodon's* large body size necessitated preying on megaherbivores for
340 adequate sustenance [3]. To do so, like most large cats today, they would have used

341 their hindlimbs for propulsion and acceleration [51–53]. This pounce behavior would
342 have been emphasized in *Smilodon*. Its ratio of total forelimb length to total hindlimb
343 length is greater than those of living felids, while its ratio of tibia length to femur length
344 ranks lower than those of living felids [14]. The shorter hindlimbs lacking the distal limb
345 elongation seen in cursorial animals suggest that *Smilodon* was an ambush predator
346 surpassing the ability of felids today [54]. Hunting large prey is dangerous [55]; after the
347 initial leap powered by its hindlimbs, *Smilodon* would have grappled with its struggling
348 prey, as evidenced by traumatic injuries radiating dorsolaterally to where the ribs
349 articulate with the spine [5]. As it subdued prey with its robust forelimbs [15,52] under
350 enough torque to injure the lumbar vertebrae [5], *Smilodon* would have needed to
351 leverage itself against the ground using its hindlimbs. Therefore, the pelvis and femur
352 would have been critical to multiple phases of *Smilodon*'s hunting strategy.

353 The dysplastic individual would have encountered much difficulty hunting in this
354 manner. Yet, as evidenced by its large size and by complete fusion of its pelvic and
355 femoral elements, it had reached adult age. (Studies of the detailed timing of epiphyseal
356 fusion in large wild cats are lacking, but distal femoral epiphyses fuse at around the
357 same time as or soon after proximal femoral epiphyses in domestic cats and dogs
358 [56,57]; given this, the broken distal end likely also had a fused epiphysis.) Adulthood in
359 *Smilodon* is likely equivalent to at least four years old, given that the forelimb and/or
360 hindlimb in the African lion completely fuses between 4.5 and 5.5 years of age [58–60];
361 this is supported by bone histological work quantifying at least four lines of arrested
362 growth (LAGs; one per growth year) in limb bones with fused epiphyses belonging to
363 *Smilodon fatalis* from the Talara asphaltic deposits in Peru [61]. Some of the LAGs in

364 the *Smilodon* histological specimens likely have been masked by secondary bone
365 remodeling [61], which may be more extensive in larger-bodied taxa [62], and these
366 specimens may be older than the number of visible LAGs suggest; therefore, the
367 pathologic specimen may be quite a bit older than four years of age.

368 To sustain growth to this age, the animal must have secured prey items without
369 necessarily hunting them. We propose that this individual, and other critically pathologic
370 *Smilodon* like it, survived to adulthood by association with a social group that assisted it
371 with feeding and protection. Evidence for sociality in *Smilodon* historically has been
372 drawn from three main sources: quantification of sexual dimorphism in the size and
373 shape of skeletal elements, ontogenetic patterns in teeth and bone, and comparisons of
374 Rancho La Brea with extant carnivore communities comprising social and solitary
375 members.

376 Extant large felids are predominantly solitary, with neighboring and often related
377 females tending to feed cooperatively more often and in larger numbers than males.
378 The pride-dwelling, male-dominated African lion is the social outlier, though African lion
379 females aggregate as well [63]. High levels of sexual dimorphism mark the African lion:
380 males have manes, larger body size, and upper canines 25% larger than in females
381 [64,65]. Rancho La Brea *Smilodon fatalis* exhibits discernible levels of sexual
382 dimorphism in its canine teeth but less pronounced than the African lion's, suggesting
383 that its social structure differed from that of *P. leo* [26]. Instead, *Smilodon* may have
384 been solitary with females occasionally sharing prey, as is the case for most extant
385 felids with low craniodental sexual dimorphism; or—if social—then its breeding system
386 likely differed from those of any large felids today [26].

387 In Rancho La Brea *Smilodon*, levels of sexual dimorphism in overall cranial
388 shape (though not size) are on par with those in extant pantherine cats, supporting the
389 existence of a social structure in *Smilodon* [66]. However, pantherines span the social
390 African lion to the solitary leopard (*Panthera pardus*), and therefore this comparison
391 generated equivocal support for solitary polygyny or unisexual groups [66]. On the other
392 hand, sexual dimorphism in various craniodental measurements for *Smilodon fatalis*
393 from Talara is greater than at RLB and more consistent with sociality; the higher
394 proportion of females to males at Talara further supports cooperative hunting among
395 females [61]. Among social carnivorans today, social structure varies by resource level:
396 larger groups during times of plenty or in the presence of competitors; pairs or
397 individuals when resources are limited [67,68]. The difference in *Smilodon* sexual
398 dimorphism between Rancho La Brea and Talara may well reflect true differences in
399 social structure stemming from differences in competitor density or resource limitation,
400 which may vary across sites or through time.

401 Ontogenetic growth patterns in teeth and bone support inferences of sociality
402 from skeletal sexual dimorphism. In *Smilodon*, the teeth appear to mature earlier than
403 when sutures and long-bone epiphyses fuse. At Rancho La Brea, most sampled
404 specimens show significant pulp cavity closure of the lower canine (14 of 19 specimens
405 over approximately 80% closure), a sign of dental maturation [69]. In contrast, RLB
406 pantherine pulp cavities compared against the *Smilodon* sample were more evenly
407 distributed across the closure percentage range—suggesting that the asphalt seeps
408 tended to trap older *Smilodon* or, more likely (because other assessments have yielded
409 estimates of a full range of ages in *Smilodon* [70]), that teeth mature earlier in *Smilodon*

410 than in pantherines. At Talara, age determination by dentition yields low estimated
411 counts of juveniles, but age determination based on limb epiphyseal fusion yields 41%
412 juveniles [61]. Histology of Talara *Smilodon* long bones reinforces this mismatch, as an
413 apparent adult femur with fused epiphyses and seven LAGs may have been still
414 growing, based on the lack of avascular and acellular subperiosteal lamellar bone [61].
415 The lag in maturation between the teeth and the limb bones suggests delayed weaning,
416 prolonged juvenile dependence, and extended familial care until the full adult hunting
417 morphology—saber canines and robust limbs—was complete. This social scenario
418 would help explain how the individual in this current study was able to survive to
419 adulthood given its debilitating handicap.

420 Lastly, the relatively high abundance of *Smilodon fatalis*—the most abundant
421 carnivoran at Rancho La Brea, second to the dire wolf—has been interpreted as
422 evidence for sociality. A full range of ages is present among Rancho La Brea *Smilodon*;
423 in contrast, animals interpreted to be solitary, such as the American lion *Panthera atrox*,
424 are represented largely by adult individuals [70]. Furthermore, the proportions of social
425 and solitary species at Rancho La Brea parallel those drawn to audio playbacks of
426 herbivore distress calls in the African savanna [24,25]. Extant social felids occur in
427 higher densities than solitary species, and multiple individuals congregate around fresh
428 kills; therefore, the high incidence of *S. fatalis* at Rancho La Brea makes sense less if it
429 were solitary and more so if it were social.

430

431 **Conclusions**

432 Novel application of computed tomography to an old question of paleopathology
433 has enabled diagnosis of hip dysplasia, a lifelong condition, in an individual *Smilodon*
434 *fatalis* saber-toothed cat, informing the longstanding debate between social and solitary
435 hypotheses for the behavior of this extinct predator. This individual likely was not the
436 only *Smilodon* afflicted with hip dysplasia and preserved by the asphalt seeps; at least
437 one other pelvic specimen—described by Shermis [23]—appears superficially similar to
438 the pelvis examined in this study, and further study may reveal it to be dysplastic as
439 well. The individual examined in this study reached adulthood (at least four to seven
440 years of age) but could never have hunted nor defended territory on its own, given its
441 locomotor impairment that would have been present since infancy. As such, this
442 individual likely survived to adulthood by association with a social group that assisted it
443 with feeding and protection.

444 Further conclusions are limited by the lack of a comprehensive and systematic
445 comparative dataset comprising pathologic postcranial specimens from extant species,
446 a persistent limitation of paleopathological studies [5]. Natural history museums may
447 acquire cranial remains from zoos or similar institutions but often lack storage to
448 accommodate postcranial skeletons, especially for large carnivores. While radiographic
449 studies on domestic cats and dogs are informative as to the nature of hip dysplasia,
450 these studies tend to examine pathologic bones *in situ*, still embedded in a muscular
451 framework, as opposed to the isolated context in which paleopathological specimens
452 are found. Computed tomography may be key to building such a dataset in the future.

453 Within the scope of this study, we cannot completely rule out the hypothesis that
454 the pathologic animal was a scavenger and therefore could have obtained food outside
455 the context of a social structure. It is also possible that, despite its disability, its large
456 body size and fearsome canines made it a strong interference competitor. However, the
457 pathologic specimens that we have examined here in detail are consistent with the
458 predominance of studies supporting a spectrum of social strategies in this extinct
459 predator. In many extant carnivores, sociality offers the benefits of cooperative hunting
460 and cooperative rearing of young [71]. These benefits likely also applied to the extinct
461 *Smilodon* in the late Pleistocene. As *Smilodon* coexisted with a rich megafaunal
462 carnivore assemblage including dire wolves, American lions, and short-faced bears,
463 cooperative sociality may have aided its success as a predator in a crowded field.

464

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471

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657
658

659 **Supporting Information**

660

661 **Movie S1.** A video movie of a structured light surface scan of LACMHC 131, the
662 pathologic pelvis belonging to *Smilodon fatalis*. Movie created in Adobe Photoshop CC
663 by Carrie Howard.

664

665 **Movie S2.** A video scrolling anteroposteriorly through LACMHC 131, the pathologic
666 pelvis belonging to *Smilodon fatalis*. Ventral is at top. Video created by Carrie Howard
667 from CT scans generated at the S. Mark Taper Foundation Imaging Center at Cedars
668 Sinai Medical Group.

669

670 **File S1.** Three-dimensional PDF of the pathologic pelvis (LACMHC 131) and femur
671 (LACMHC 6963).

672

673 **Dataset S1.** Compressed zip file containing the full computed tomography scan of
674 LACMHC 131, the pathologic pelvis.

675

676 **Dataset S2.** Compressed zip file containing the full computed tomography scan of
677 LACMHC 6963, the pathologic femur.

678

679 **Dataset S3.** Compressed zip file containing the full computed tomography scan of
680 LACMHC K-3232, the non-pathologic right femur.



Figure 1

A

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B



3 cm

C



D



E



F



3 cm

Figure 2



Figure 3

A



B



3 cm

C



D



E



F



3 cm

Figure 4