Research Square

Preprints are preliminary reports that have not undergone peer review.
They should not be considered conclusive, used to inform clinical practice,
or referenced by the media as validated information.

How to survive as mountain dwellers: palaeopathological study of European leopards

Joan Madurell-Malapeira
jmadurell@gmail.com

Università di Firenze

Maria Prat-Vericat
Conflent Spéléo Club

Saverio Bartolini-Lucenti
Università di Firenze

Darío Fidalgo
Museum für Naturkunde - Leibniz Institute for Research on Evolution and Biodiversity

Natalia V. Serdyuk
Russian Academy of Sciences

Alexander Lavrov
Russian Academy of Sciences

Isaac Rufí
University of Barcelona

Esteban Messeguer
Associació Paleontològica de Vinaròs

Nil Ramada
Autonomous University of Barcelona (UAB)

Leopoldo Pérez
Universidad de La Laguna (ULL), La Laguna (Tenerife)

Celia Díez-Canseco
Autonomous University of Barcelona (UAB)

Carles Tornero
Autonomous University of Barcelona (UAB)

Research Article

Keywords: Panthera pardus, Paleopathology, Fracture healing, Computed tomography, Late Pleistocene, Pyrenees

Posted Date: November 14th, 2026

DOI: https://doi.org/10.21203/rs.3.rs-11577530/v1

License: This work is licensed under a Creative Commons Attribution 4.0 International License.
Read Full License

Additional Declarations: No competing interests reported.

How to survive as mountain dwellers: palaeopathological study of European leopards

Joan Madurell-Malapeira[1,2,3*], Maria Prat-Vericat[3], Saverio Bartolini-Lucenti[1], Darío Fidalgo[4], Natalia V. Serdyuk[5], Alexander Lavrov[5], Isaac Rufí[6], Esteban Messeguer[7], Nil Ramada[8], Leopoldo Pérez[9,2], Celia Díez-Canseco[8,2], Carles Tornero [8,2]

[1]Earth Sciences Department, Paleo[Fab]Lab, Università di Firenze, Via G. La Pira 4, 50121 Firenze, Italy
[2]Institut Català de Paleoecologia Humana i Evolució Social (IPHES-CERCA), Zona Educacional 4, Campus Sescelades URV (Edifici W3), 43007, Tarragona, Spain
[3]Conflent Spéléo Club, 4, Traverse Des Fabriques, 66500 Prades de Conflent, France
[4]Museum für Naturkunde - Leibniz Institute for Research on Evolution and Biodiversity, Berlin, Germany
[5]Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, Russia
[6]SERP, Department of History and Archaeology, University of Barcelona, C/Montalegre, 6-8, 08001 Barcelona
[7]Associació Paleontològica de Vinaròs, C/ Almería 1. Vinaròs, Spain.
[8]Department of Prehistory, Autonomous University of Barcelona (UAB), Bellaterra, ES, Spain.
[9] Área de Prehistoria, Departamento de Geografía e Historia, Facultad de Humanidades, Universidad de La Laguna (ULL). Campus de Guajara. 38200, La Laguna (Tenerife), Spain
.
* Corresponding author: Joan Madurell-Malapeira (jmadurell@gmail.com)

Abstract

Previous morphofunctional analyses linked Pleistocene leopards from the eastern Pyrenees to rocky mountainous habitats, within a broader interpretation of European leopard ecology. Such environments are expected to increase exposure to falls, missteps and difficult landings during locomotion and prey capture. Here we develop the palaeopathological dimension of this interpretation by examining two pathological leopard (*Panthera pardus*) forelimb elements from Late Pleistocene European cave assemblages: a radius from Grotte de la Carrière, France, and a fifth metacarpal from Tut de Fustanyà, Iberia. External morphology and computed-tomography images reveal pronounced diaphyseal enlargement, irregular periosteal bone formation, cortical reorganization and persistent deformation, most consistent with remodeled fractures. Substantial reparative bone documents survival beyond the acute injury and through an extended phase of osseous repair. Comparisons with pathological leopards, lynxes, cave lions and saber-toothed felids support the diagnostic assessment and place these injuries within a broader record of skeletal trauma. We propose that the fractures reflect the mechanical risks of locomotion and hunting in steep, rocky terrain. The pathological evidence adds an individual life-history dimension to the postcranial adaptations previously recognized in European leopards. Integrating the lesions with the morphological and environmental evidence, we interpret them as potential traumatic consequences of the mountain-associated way of life proposed for European Pleistocene leopards. Their extensive repair also documents the capacity of injured individuals to survive within this demanding ecological setting.

Keywords *Panthera pardus* · Paleopathology · Fracture healing · Computed tomography · Late Pleistocene · Pyrenees

Introduction

The ecology of Pleistocene European leopards has recently been interpreted in relation to a preference for mountainous and rocky environments, supported by postcranial anatomy, geographical distribution and palaeoecological comparisons (Prat-Vericat et al. 2025). This interpretation raises a complementary question about the physical consequences of exploiting such habitats. Locomotor adaptations that facilitate movement and prey capture on steep and irregular substrates may coexist with exposure to falls and other accidents. Pathological bones provide a means of examining injuries and survival within this ecological model.

Paleopathological remains preserve aspects of an animal's life history that cannot be reconstructed from healthy anatomy alone. A healed lesion records both an injury or disease process and a biological response, providing evidence that the individual survived at least part of its subsequent functional consequences. In carnivores, this type of observation is particularly relevant due to their active foraging behaviour, which involves direct interaction with other animals. Reliable interpretation requires a distinction between the lesion itself, its likely pathological origin and the behavioral circumstances in which it developed (Lovell 1997; Rothschild and Martin 2006).

Felid forelimbs contribute to body support and locomotion as well as to grasping and restraining prey. Comparative anatomy links aspects of forelimb construction to prey-size preferences, making injuries to the radius and manus particularly informative for evaluating potential functional limitations (Meachen-Samuels and Van Valkenburgh 2009). At Rancho La Brea (California, USA), differences in the skeletal distribution of trauma between *Smilodon fatalis* and dire wolves have been interpreted in relation to their contrasting predatory strategies (Brown et al. 2017). Complementary studies of tooth breakage demonstrate that dental damage also contains information about feeding ecology (Van Valkenburgh and Hertel 1993; Van Valkenburgh 2009).

The European record provides several relevant examples of pathological felids. Pleistocene cave lions preserve healed fractures and other skeletal abnormalities, including a callused rib from Sloup Cave (Czech Republic; Rothschild and Diedrich 2012). A pathological scapula of *Homotherium latidens* from Schöningen (Germany) records shoulder osteoarthritis with trauma, ageing or their combined effects considered as possible causes (Janssens et al. 2019). More recently, a displaced and healed fifth-metacarpal fracture, together with changes in adjacent

metacarpals, was described in the Early Pleistocene lynx from Taurida Cave, Crimea (Serdyuk et al. 2025). These cases illustrate both survival with skeletal lesions and the diversity of processes represented by abnormal bone morphology.

Pathological remains are also known in older European felids. The Late Miocene saber-toothed felid *Promegantereon ogygia*, includes healed metatarsal injuries from Batallones-1 (Iberia; Salesa et al. 2006; Salesa et al. 2014). A radius of the same species from La Roma 2 (Iberia) was interpreted as showing tendon-related ossification associated with the abductor pollicis longus, rather than a shaft fracture (Salesa et al. 2014). In *Machairodus aphanistus*, also from Batallones-1, a proliferative calcaneal lesion, metacarpal osteosclerosis and a mandibular abscess were evaluated through separate differential diagnoses (Salesa et al. 2024). These Miocene examples provide a useful comparative framework, while remaining distinct from the Pleistocene occurrences considered here.

Leopard palaeopathology is less extensively documented. A proximal radius of *Panthera pardus* from Biśnik Cave (Poland), bears a porous excrescence at the radial tuberosity, but the fragmentary specimen provided no unequivocal evidence of a fracture and its etiology remained unresolved (Marciszak et al. 2011). This record establishes that skeletal abnormalities in European fossil leopards have received previous attention, while also showing why an external proliferation should not automatically be described as fracture callus. Internal imaging can materially improve diagnosis: computed tomography of a pathological *Smilodon* pelvis and associated femur favored developmental hip dysplasia over earlier traumatic or infectious interpretations (Balisi et al. 2021).

Leopards were geographically widespread in Pleistocene Europe, although their fossil record is uneven and consists largely of material from cave deposits. Iberian records document the species in both archaeological and palaeontological contexts, while ancient DNA reveals a more complex Eurasian population history than can be reconstructed from morphology alone (Sanchís et al. 2015; Paijmans et al. 2018). Prat-Vericat et al. (2025) combined the eastern Pyrenean assemblages with a broader European comparative sample and identified hindlimb, tarsal and metapodial characteristics resembling those of the snow leopard (*Panthera uncia*). We interpreted this combination of traits as facilitating powerful jumps, stability and prey capture in rugged mountain environments. Together with the geographical distribution and palaeoecological evidence, these results supported preferential exploitation of mountainous habitats, including montane forests and rocky terrain with steep cliffs, particularly during the Late Pleistocene.

This mountain ecology model predicts repeated exposure to mechanically demanding situations. Hunting caprines and moving across broken slopes would require secure footing,

precise jumps and controlled landings, with a risk of sudden loading when a step or landing failed (Prat-Vericat et al. 2025). Fractures affecting the forelimb are therefore relevant to the potential costs of this habitat use. Their occurrence, morphology and repair can be evaluated alongside the functional evidence to investigate how the exploitation of rugged terrain may have shaped individual life histories.

Here we extend the ecological interpretation developed by Prat-Vericat et al. (2025) through a palaeopathological study of a radius from Grotte de la Carrière (France) and a fifth metacarpal from Tut de Fustanyà (Iberia). We describe the lesions, evaluate a traumatic interpretation against alternative diagnoses and compare them with pathological European felids.

Materials and Methods

Research framework

The study concerns two *Panthera pardus* forelimb elements with pathologies: a right radius (GDC2021-S2-P30-624-Nv.2) from Grotte de la Carrière and the left fifth metacarpal (RO25-834-Mg-03) from Tut de Fustanyà. In the following analyses, the specimens are treated as separate cases from distinct localities. Their taxonomic context follows the regional assessment of Pyrenean leopard remains, while comparisons of pathological morphology are drawn from published descriptions and illustrations of fossil and living felids.

The assessment focuses on the position and extent of bone proliferation, alteration of shaft alignment, preservation of cortical boundaries, internal cavities and evidence of integration between the original shaft and newly formed bone. The diagnostic approach follows established paleopathological principles and considers fracture repair, infection, neoplasia and other causes of localized bone formation (Lovell 1997; Rothschild and Martin 2006). Comparative examples are used to evaluate morphological alternatives and functional implications; they are not treated as equivalent cases merely because an element is enlarged or deformed.

Grotte de la Carrière

Grotte de la Carrière forms part of the Réseau Lachambre in Les Gorges de Villefranche, in the Têt Valley of the eastern French Pyrenees. The cave lies at approximately 540 m above sea level and contains fossiliferous deposits sampled in two distinct excavation areas, Sondage 1 and Sondage 2. Sondage 2, situated in the main gallery, contains a Late Pleistocene assemblage assigned to MIS 3, around 47 ka (Prat-Vericat et al. 2025).

The Grotte de la Carrière collection is under the supervision of the Direction régionale des affaires culturelles (DRAC) Occitanie and the Conflent Spéléo Club de Prades (Prat-Vericat et al. 2025).

Tut de Fustanyà

Tut de Fustanyà is a karstic cavity in the Freser Valley near Queralbs, Ripollès, Girona, on the southern side of the eastern Pyrenees. Its approximately 16 m horizontal gallery opens towards the southwest at about 1130 m above sea level. Excavations in 1973, 1974 and 1978 recovered Middle Palaeolithic artefacts and faunal remains, including *Panthera pardus*, from Sector 3 in the inner part of the gallery. The cave also contains younger archaeological material, including Holocene and Bronze Age remains, which should be distinguished from its Pleistocene faunal deposits. Excavations resumed in 2022 and documented a preserved Late Pleistocene sequence (Prat-Vericat et al. 2025).

Prat-Vericat et al. (2025) reported accelerator mass spectrometry radiocarbon determinations of 28,235 ± 143 and 31,604 ± 168 uncalibrated ^{14}C yr BP for TUT22-101-224 and TUTnd-sup-5, respectively, with uncertainties expressed at 1σ.

The collection recovered during the 2022–2025 campaigns and housed at the Institut Català de Paleoecologia Humana i Evolució Social (IPHES-CERCA), Tarragona (Prat-Vericat et al. 2025). The pathological fifth metacarpal is retained there under its supplied inventory, RO25-834-Mg-03.

Imaging and diagnostic assessment

The internal structure of both pathological specimens was investigated using X-ray computed tomography (CT). The right radius from Grotte de la Carrière (GDC2021-S2-P30-624-Nv.2) was scanned using a 16-slice helical CT scanner (Brivo CT385, GE Healthcare) at the Hospital Clínic Veterinari, Universitat Autònoma de Barcelona, Bellaterra, Spain. The left fifth metacarpal from Tut de Fustanyà (RO25-834-Mg-03) was examined using a GE Phoenix v|tome|x s 240 micro-computed tomography system at the Centro Nacional de Investigación sobre la Evolución Humana (CENIEH), Burgos, Spain. Longitudinal and transverse sections were examined to assess fracture morphology, cortical continuity, medullary architecture and bone remodelling. The approximate positions of the illustrated sections are indicated on the corresponding three-dimensional surface models in Figs. 1 and 2.

The comparison is qualitative and concerns gross bone architecture. Particular attention was paid to changes in cortical continuity and alignment, the distribution of compact and porous tissue, and connections across the affected shaft segment. A traumatic interpretation was favored when these features jointly indicated reparative integration around a deformed diaphysis. Periosteal proliferation or increased radiopacity alone was not considered diagnostic of a fracture. Such caution is supported by CT reassessments and differential studies of other fossil felids (Balisi et al. 2021; Salesa et al. 2024).

Possible infectious changes were assessed through the presence or absence of recognizable destructive lesions, sequestra and drainage channels, while considering that a previous infection

may leave incomplete or ambiguous evidence (Lee et al. 2016). Sharp internal cracks were evaluated separately from integrated reparative tissue because fossil breakage and post-depositional alteration can mimic unhealed discontinuities. Attenuation differences were interpreted as structural features rather than measurements of original bone mineral density.

Results

Pathological radius from Grotte de la Carrière

The studied radius preserves its proximal and distal epiphysis and exhibits marked deformation of the middle to distal diaphysis (Fig. 1A–D). A large, asymmetric bony expansion interrupts the normal shaft outline. The enlarged segment has irregular margins and a surface that combines relatively smooth areas with rough projections and depressions. The unaffected portions of the shaft remain recognizable above and below the lesion, but their alignment through the expanded region is altered. The external deformation therefore comprises both increased shaft breadth and a change in its longitudinal architecture.

Longitudinal CT sections show substantial mineralized tissue around the deformed shaft, with irregular cortical boundaries and a heterogeneous internal network of cavities and trabecular structures (Fig. 1E, F). Parts of the original cortical outline remain recognizable within the enlargement, alongside additional bone that connects the affected region. Transverse sections reveal an irregular expanded perimeter and internal spaces of differing size and position (Fig. 1G, H). The pathological mass is not uniformly solid, and residual cavities should be distinguished from the surrounding compact and trabecular tissue.

Together, the external and internal observations document localized bone proliferation integrated with a markedly deformed diaphysis. They support substantial osseous repair around a previous shaft injury. The persistence of deformation and heterogeneous architecture indicates that healing did not restore the original shape.

Pathological fifth metacarpal from Tut de Fustanyà

The fifth metacarpal retains recognizable proximal and distal epiphysis, but an extensive, irregular enlargement occupies much of its diaphysis (Fig. 2A–F). The swelling is elongated along the shaft and is particularly conspicuous relative to the narrower distal portion. Its external surface is rough and locally porous, and the contour differs between the complementary views. The relationship between the articular ends and the intervening shaft is deformed, with pronounced curvature near the distal part of the pathological expansion.

Longitudinal CT sections show dense cortical tissue associated with a broad zone of porous bone and internal cavities (Fig. 2G–I). Cortical boundaries can be followed through parts of the specimen, while the enlarged region displays substantial reorganization and additional

mineralized tissue around the original shaft. The medullary space is irregular and locally constricted, but remains visible in several sections. Transverse images likewise show variation in the balance between compact tissue, porous peripheral bone and central cavities (Fig. 2J–L). Thin, sharply bounded internal fissures are also present and distinguished from the more extensive integrated bony reaction.

The principal features are therefore an enlarged and deformed shaft, extensive bone deposition and reorganized internal architecture. In combination, they are consistent with a remodeled diaphyseal injury and substantial reparative callus. The specimen does not preserve the soft tissues or associated metacarpals needed to assess the full extent of the original injury to the manus.

Discussion

Interpretation of the lesions and differential diagnosis

A remodeled traumatic fracture is the most plausible explanation for each lesion. This interpretation rests on the combined evidence of localized diaphyseal expansion, altered shaft architecture and integration of newly formed bone with the affected segment. Callus formation can stabilize a fracture even when the original alignment is not restored, producing an enlarged, persistently deformed bone. Subsequent remodeling modifies the balance between cortical and trabecular tissue and can obscure the original fracture surfaces (Lovell 1997; Rothschild and Martin 2006; Einhorn and Gerstenfeld 2015). The Pyrenean specimens are consistent with this sequence, but the available evidence does not justify reconstructing a specific transverse, oblique or comminuted fracture pattern.

The interpretation of repair also requires care in describing its endpoint. A large mineralized callus demonstrates a substantial biological response, but its size is not a direct measure of healing duration, original trauma severity or final strength. Persistent deformity can coexist with union, and the restoration of bony continuity does not imply recovery of normal limb mechanics. Fracture repair is influenced by stability, vascular supply and biological condition, while later remodeling can continue after functional use resumes (Einhorn and Gerstenfeld 2015). Accordingly, the studied specimens are described as showing advanced osseous repair and remodeling, without asserting complete functional recovery or assigning a minimum survival time in weeks or months.

Infection is an important alternative or associated process because osteomyelitis can combine bone proliferation with cortical destruction. No unequivocal sequestrum or drainage channel is evident in the studied material. This reduces the positive evidence for chronic suppurative infection but does not exclude an earlier secondary infection of a fracture. Moreover, periosteal

reaction and increased bone formation are nonspecific findings that can accompany several disorders (Lee et al. 2016). A traumatic lesion and infection should therefore not be treated as mutually exclusive diagnoses solely based on the external swelling.

A proliferative neoplasm is less strongly supported than repair around a deformed shaft, although morphology alone cannot eliminate every benign or malignant lesion. The extent of preserved cortical architecture and the relationship of the proliferation to the shaft favor a reparative explanation. Similarly, the principal abnormality is diaphyseal rather than centered on an articular surface, making primary degenerative joint disease a less satisfactory explanation for the main swelling. The calcaneal and metacarpal lesions described in *Machairodus* illustrate why enlargement, sclerosis and new bone formation need to be interpreted in their anatomical settings (Salesa et al. 2024).

Tendon or ligament injury, stress-related changes and a fracture through previously diseased bone also merit consideration. A focal insertional lesion would not readily explain the full extent of the deformed diaphyseal architecture in these specimens. Nevertheless, an isolated radius or metacarpal does not reveal the condition of the entire skeleton, so systemic or metabolic disease cannot be rejected merely because only one abnormal element is available. The preferred diagnosis is therefore a remodeled fracture, with residual uncertainty concerning its precise configuration and any contributing pathology (Lovell 1997; Rothschild and Martin 2006).

Comparison with other pathological European felids

The leopard radius from Biśnik Cave (Poland) provides a particularly relevant species-level comparison. Its porous excrescence is situated at the radial tuberosity, and no fracture or bite damage was identified. Marciszak et al. (2011) explicitly left its aetiology open because preservation was incomplete. The Grotte de la Carrière radius differs in the extensive involvement of the shaft and the internal evidence of repair accompanying deformation. The comparison supports recognizing a leopard-specific paleopathological record, while avoiding the assumption that two proliferative radial lesions necessarily represent the same disease or injury.

The closest anatomical comparator for the Tut de Fustanyà specimen is the fifth metacarpal of *Lynx* from Taurida Cave. Serdyuk et al. (2025) described a displaced healed fracture with callus and deformation, together with periosteal changes affecting neighboring metacarpals. Both cases document substantial pathology in the lateral manus and survival during bone repair. However, the Taurida material includes associated metacarpals, whereas the Tut element is considered in isolation. The latter consequently offers less information on the distribution of injury across the manus or on possible compensatory changes in neighboring bones.

European cave lions broaden the comparison beyond the forelimb. The callused rib from Sloup (Czech Republic) and other lesions reviewed by Rothschild and Diedrich (2012) show that both

injury and non-traumatic skeletal abnormalities occurred in Pleistocene large felids. These cases support comparisons of lesion morphology and repair, but specific proposed aggressors or behavioral events remain interpretations. The shoulder osteoarthritis of *Homotherium* from Schöningen (Germany) makes the same distinction especially clear: an osteophyte and a subchondral cystic lesion supported the diagnosis, whereas the role of trauma, ageing and clinical symptoms remained less certain (Janssens et al. 2019).

The Miocene cases are informative about the range of lesions that can affect comparable anatomical systems. Healed metatarsal damage in *Promegantereon* from Batallones-1 (Iberia) shows survival following injury to the autopodium, while the La Roma 2 (Iberia) radial lesion demonstrates that tendon-related ossification can produce an abnormal bony outgrowth without a diaphyseal fracture (Salesa et al. 2006, 2014). These examples strengthen a lesion-specific approach to the Pyrenean material. Their value is diagnostic and functional; their different ages, body plans and environmental settings do not establish shared causes of injury or equivalent ecological responses.

Survival and functional consequences

The clearest biological inference is that both individuals survived the initial injury and a substantial period of bone formation. This is a record of survival during repair, irrespective of whether either animal ultimately regained normal performance. A radial shaft injury would be expected to compromise forelimb support and force transmission, whereas damage to a fifth metacarpal could affect the lateral manus during stance and prey restraint. However, the condition of the ulna, neighboring metacarpals, joints and soft tissues would influence the degree of impairment. Those anatomical relationships cannot be reconstructed fully from the isolated elements.

Living felids demonstrate that significant injury can be compatible with continued survival and reproduction. García-Perea (2000) documented Iberian lynxes that had recovered in the wild from serious injuries, including limb loss. More recent tracking of severely injured felids recorded continued space use and activity in Iberian lynx, bobcat and snow leopard (Nájera et al. 2024). These observations are useful analogues for persistence with impairment, but their circumstances differ: the Iberian lynxes underwent surgery and rehabilitation, while the bobcat was encountered with an already self-healed traumatic limb loss. They should not be treated as equivalent examples of completely unaided fracture recovery.

Leopard feeding ecology offers plausible routes by which an injured individual could continue obtaining food. The species uses a broad prey spectrum and can combine hunting with opportunistic exploitation of carcasses (Bailey 1993; Sunquist and Sunquist 2002). Changes in prey choice, movement or food acquisition could therefore contribute to survival during

recovery. These possibilities remain hypotheses for the fossil individuals, however. Neither callus morphology nor survival identifies the food consumed, the frequency of successful hunts or the extent to which scavenging compensated for reduced mobility. The fossils demonstrate a biological outcome, while the behavioral route to that outcome remains unresolved.

Leopard-associated assemblages at Los Rincones, Racó del Duc and S'Espasa demonstrate how prey transport and repeated cave use can contribute to fossil accumulations (Sauqué et al. 2014; Sauqué and Sanchis 2017; Sauqué et al., 2018). At Grotte de la Carrière, Prat-Vericat et al. (2025) proposed that the studied injured leopard could have used the bear-occupied cavity as a refuge and exploited bear remains. The paleopathological assessment makes survival with a damaged forelimb credible, but does not identify that individual's cave-use behavior or attribute associated feeding traces to it. Spatial association, skeletal pathology and evidence of carcass exploitation need to be assessed separately before they are combined into a reconstruction of one animal's life history.

Survival after injury also does not require a particular social system. It can reflect individual behavioral flexibility, remaining locomotor capacity and access to food, and does not on its own demonstrate provisioning by conspecifics. Likewise, an irregular or thickened shaft should not be interpreted simply as a stronger functional equivalent of normal anatomy. Comparative work on carnivoran forelimbs shows that shape reflects several interacting influences, including body size and phylogeny (Martín-Serra et al. 2014). In these specimens, pathological thickening is an acquired response to injury and its effect on performance would require evidence beyond external robustness.

Mountain ecology and the mechanical risks of life in rocky terrain

The principal ecological interpretation of these lesions follows directly from the study of Prat-Vericat et al. (2025). Our former analysis of Pyrenean and other European leopards identified postcranial similarities with snow leopards, particularly in hindlimb proportions, the tarsus and several metapodial indices. The relatively high crural indices, tarsal morphology and robust metapodials were interpreted together as adaptations favoring jumping, stability and prey capture in rugged mountain environments. The paleogeographical distribution and associated prey evidence reinforced this interpretation. The fractures described here extend that reconstruction by documenting substantial traumatic damage in populations associated with these habitats and by allowing the possible physical costs of their locomotor ecology to be considered alongside their functional adaptations (Fig. 3).

Extant African leopards provide a comparative context for interpreting the injuries described here. In a retrospective series of 61 free-ranging leopards from the Greater Kruger National Park, South Africa, Mitchell et al. (2026) recorded traumatic injuries in 25 individuals (41%), including

bite wounds attributed to conspecifics, lions and hyaenas, porcupine-quill injuries, rib fractures in three animals and a fractured tarsus. Two healed ribs in one individual document survival after skeletal trauma, while canine fractures were recorded in eight animals. Other findings included hip arthrosis, skull lesions attributed to tuberculous osteomyelitis, and pulmonary, renal and vascular abnormalities, many of the visceral changes being considered incidental. One individual had no recorded non-parasitic conditions. No comparable healed radial or metacarpal shaft fractures were reported, although incomplete anatomical coverage precludes interpreting this as a true absence. These observations document both injury and skeletal repair in living African leopards, with aggressive encounters and potentially prey capture contributing to trauma. Against this background, we propose that repeated movement and prey capture on steep, irregular substrates exposed Pleistocene Pyrenean leopards to additional mechanical hazards.

Regular movement across steep slopes, rocky ledges and uneven substrates would have required controlled climbing, descent and landing, including during the pursuit and restraint of prey. We propose that repeated exposure to these situations increased opportunities for falls, loss of footing and awkward landings, even in animals anatomically adapted to mountain locomotion. A failed landing could impose sudden compression and bending on the radius, while an irregular contact or trapped manus could concentrate loads on individual metacarpals (Fig. 3). The dual role of felid forelimbs in support and prey restraint makes both locomotor accidents and hunting on difficult terrain relevant to these injuries (Meachen-Samuels and Van Valkenburgh 2009). This provides a mechanistic explanation for how the habitats reconstructed by Prat-Vericat et al. (2025) could contribute to forelimb fractures.

The distribution of damage in the two specimens is compatible with this interpretation. Both lesions affect the diaphysis of a forelimb element and preserve deformation associated with extensive repair. We interpret these features as evidence of traumatic events whose consequences are consistent with the falls, missteps or forceful landings predicted by the mountain ecology model (Fig. 3). Prey capture and terrain-related injury can also interact: restraining or transporting prey on an uneven slope may combine resistance from the prey with instability of the supporting limb. The new observations therefore connect the previously inferred locomotor adaptations with injuries that could arise during the activities those adaptations facilitated.

Sampling limits and contribution to felid palaeobiology

The proposed association between mountain habitat use and trauma concerns ecological interpretation; the two selected pathological elements do not establish a higher fracture frequency than in leopards from less rugged habitats. Nor can their remodeled morphology

identify the particular accident or exclude prey-inflicted trauma and aggressive encounters. Testing the prediction of increased injury risk requires standardized comparisons among habitats, including counts of unaffected elements and comparable recording of skeletal regions, as illustrated by the broader comparative approach at Rancho La Brea (USA; Brown et al. 2017). The present contribution is a qualitative link between documented injuries and the mountain ecology supported by the regional anatomical and palaeoecological evidence.

The preservation of repaired lesions also selects individuals that survived long enough to form recognizable new bone. Rapidly fatal trauma may leave less diagnostic evidence of an antemortem event, while later breakage can obscure both healed and unhealed injuries. The observed record consequently represents a subset of the injuries that occurred in the living population (Lovell 1997). This limitation affects behavioral interpretation as well as comparisons among assemblages and should be considered before treating an apparent absence of lesions as evidence of low injury risk.

Conclusions

The radius from layer 2 of Grotte de la Carrière Sondage 2 and the fifth metacarpal from Tut de Fustanyà, both from the Late Pleistocene of the Pyrenees, exhibit extensive diaphyseal bone proliferation, deformation and internal reorganization. Their combined external and tomographic morphology is most consistent with remodeled fractures, documenting survival beyond the acute injury and through substantial osseous repair. Comparisons with pathological European felids strengthen this assessment. These findings provide the palaeopathological continuation of the morphofunctional and palaeoecological study by Prat-Vericat et al. (2025), adding evidence of injury and recovery to the reconstruction of Pyrenean and European Pleistocene leopards as inhabitants of mountainous and rocky environments.

Within this ecological model, regular movement and prey capture on steep, rocky substrates would have exposed leopards to falls, unstable footing and difficult landings. We propose that the fractures described here reflect these mechanical hazards and illustrate potential traumatic consequences of a mountain-associated lifestyle. Their repair also records the capacity of injured individuals to survive within this demanding setting. The study therefore develops the interpretation of European Pleistocene leopards as mountain dwellers by integrating the possible costs of locomotion and hunting in rugged terrain with the previously documented anatomical adaptations that enabled them to exploit these environments.

Acknowledgements The authors want to thank Alfred Sanchís and Antonio Rodriguez-Hidalgo for various support during the research process.

Authors contributions J.M.-M. prepared the first draft of the manuscript. All authors reviewed and improved the manuscript different versions. J.M.-M. prepared the figures. All authors read and agreed to the definitive version of the manuscript.

Funding Research at the Réseau Lachambre was funded by the Direction Regionalle des Affaires Culturelles de Montpellier (DRAC, Occitanie) under different research projects leaded by J.M.-M. Research at Tut de Fustanyà was framed in the ARRELS project: 'Arrels prehistòriques de la transhumància a l'alt Ripollès: projecte arqueològic 2022–2025' (CLT009/ 22/000042), financed by Departament de Cultura, Generalitat de Catalunya (PI: Carlos Tornero). L.P. is supported by a postdoctoral contract funded by the University of La Laguna, "La Caixa" Banking Foundation and the "Cajacanarias" Banking Foundation, and is part of the research group "PAST: Prehistory and Archaeology of Time and Space" at the same university.

Data availability

The morphological observations supporting this study are documented in the specimen descriptions and Figs. 1 and 2. The sources of contextual and comparative information are cited in the text.

References

Bailey TN (1993) The African leopard: ecology and behavior of a solitary felid. Columbia University Press, New York. https://doi.org/10.7312/bail90198

Balisi MA, Sharma AK, Howard CM, Shaw CA, Klapper R, Lindsey EL (2021) Computed tomography reveals hip dysplasia in the extinct Pleistocene saber-tooth cat *Smilodon*. Sci Rep 11:21271. https://doi.org/10.1038/s41598-021-99853-1

Blanco RE, Luzardo-Vera DE (2021) A biomechanical model to assess the injury risk of leopards (*Panthera pardus*) hunting by free falling from trees. Biol Commun 66:236–244. https://doi.org/10.21638/spbu03.2021.305

Brown C, Balisi M, Shaw CA, Van Valkenburgh B (2017) Skeletal trauma reflects hunting behaviour in extinct sabre-tooth cats and dire wolves. Nat Ecol Evol 1:0131. https://doi.org/10.1038/s41559-017-0131

Einhorn TA, Gerstenfeld LC (2015) Fracture healing: mechanisms and interventions. Nat Rev Rheumatol 11:45–54. https://doi.org/10.1038/nrrheum.2014.164

García-Perea R (2000) Survival of injured Iberian lynx (*Lynx pardinus*) and non-natural mortality in central-southern Spain. Biol Conserv 93:265–269. https://doi.org/10.1016/S0006-3207(99)00142-1

Janssens LAA, Verheijen IKA, Serangeli J, van Kolfschoten T (2019) Shoulder osteoarthritis in a European saber-toothed cat (*Homotherium latidens*) from the Lower Palaeolithic site of Schöningen (Germany). Int J Paleopathol 24:279–285. https://doi.org/10.1016/j.ijpp.2018.06.002

Lee YJ, Sadigh S, Mankad K, Kapse N, Rajeswaran G (2016) The imaging of osteomyelitis. Quant Imaging Med Surg 6:184–198. https://doi.org/10.21037/qims.2016.04.01

Lovell NC (1997) Trauma analysis in paleopathology. Am J Phys Anthropol 104(S25):139–170. https://doi.org/10.1002/(SICI)1096-8644(1997)25%2B%3C139::AID-AJPA6%3E3.0.CO;2-%23

Marciszak A, Krajcarz MT, Krajcarz M, Stefaniak K (2011) The first record of leopard *Panthera pardus* Linnaeus, 1758 from the Pleistocene of Poland. Acta Zool Cracov 54A:39–46. https://doi.org/10.3409/azc.54a_1-2.39-46

Martín-Serra A, Figueirido B, Palmqvist P (2014) A three-dimensional analysis of morphological evolution and locomotor performance of the carnivoran forelimb. PLoS ONE 9:e85574. https://doi.org/10.1371/journal.pone.0085574

Meachen-Samuels J, Van Valkenburgh B (2009) Forelimb indicators of prey-size preference in the Felidae. J Morphol 270:729–744. https://doi.org/10.1002/jmor.10712

Mitchell EP, de Klerk-Lorist LM, Buss P, Reininghaus B, Bengis R (2026) Pathological findings in 61 free-ranging leopards (*Panthera pardus*) from the Greater Kruger National Park, South Africa. Part Two: non-parasitic conditions. J Comp Pathol 228:45–52. https://doi.org/10.1016/j.jcpa.2026.04.010

Nájera F, Uiterwaal SF, Crespo E, Grande-Gómez R, Sánchez JF, Mata-Huete M, Palmer J, Iturrarte G, Peña J, Munkhtsog B, Munkhtsog B, Poyarkov AD, Hernandez-Blanco JA, Alexandrov DY, Galsandorj N, Deem SL (2024) Insights into the spatial ecology of severely injured free-living felids: Iberian lynx, bobcat, and snow leopard. Ecol Evol 14:e11000. https://doi.org/10.1002/ece3.11000

Paijmans JLA, Barlow A, Förster DW, Henneberger K, Meyer M, Nickel B, Nagel D, Havmøller RW, Baryshnikov GF, Joger U, Rosendahl W, Hofreiter M (2018) Historical biogeography of the leopard (*Panthera pardus*) and its extinct Eurasian populations. BMC Evol Biol 18:156. https://doi.org/10.1186/s12862-018-1268-0

Prat-Vericat M, Marciszak A, Bartolini-Lucenti S, Fidalgo D, Rufí I, Tura-Poch C, Vizcaíno-Varo V, Jovells-Vaqué S, Ramada N, Díez-Canseco C, Gelabert P, Tornero C, Terradas X, Rook L, Madurell-Malapeira J (2025) A review on Pyrenean Pleistocene leopards paleoecology, paleobiogeography and adaptative convergences with snow leopards. Quat Sci Rev 358:109327. https://doi.org/10.1016/j.quascirev.2025.109327

Rothschild BM, Diedrich CG (2012) Pathologies in the extinct Pleistocene Eurasian steppe lion *Panthera leo spelaea* (Goldfuss, 1810)—Results of fights with hyenas, bears and lions and other ecological stresses. Int J Paleopathol 2:187–198. https://doi.org/10.1016/j.ijpp.2012.09.004

Rothschild BM, Martin LD (2006) Skeletal impact of disease. New Mexico Museum of Natural History and Science, Bulletin 33, Albuquerque

Salesa MJ, Antón M, Turner A, Morales J (2006) Inferred behaviour and ecology of the primitive sabre-toothed cat *Paramachairodus ogygia* (Felidae, Machairodontinae) from the Late Miocene of Spain. J Zool 268:243–254. https://doi.org/10.1111/j.1469-7998.2005.00032.x

Salesa MJ, Antón M, Siliceo G, Pesquero MD, Alcalá L (2014) First evidence of pathology in the forelimb of the Late Miocene saber-toothed felid *Promegantereon ogygia* (Machairodontinae, Smilodontini). Anat Rec 297:1090–1095. https://doi.org/10.1002/ar.22902

Salesa MJ, Hernández B, Marín P, Siliceo G, Martínez I, Antón M, García-Real MI, Pastor JF, García-Fernández RA (2024) New insights on the ecology and behavior of *Machairodus aphanistus* (Carnivora, Felidae, Machairodontinae) through the paleopathological study of the fossil sample from the Late Miocene (Vallesian, MN 10) of Cerro de los Batallones (Torrejón de Velasco, Madrid, Spain). J Mamm Evol 31:21. https://doi.org/10.1007/s10914-024-09721-8

Sanchis A, Tormo C, Sauqué V, Sanchis V, Díaz R, Ribera A, Villaverde V (2015) Pleistocene leopards in the Iberian Peninsula: new evidence from palaeontological and archaeological contexts in the Mediterranean region. Quat Sci Rev 124:175–208. https://doi.org/10.1016/j.quascirev.2015.07.013

Sauqué V, Sanchis A (2017) Leopards as taphonomic agents in the Iberian Pleistocene, the case of Racó del Duc (Valencia, Spain). Palaeogeogr Palaeoclimatol Palaeoecol 472:67–82. https://doi.org/10.1016/j.palaeo.2017.01.016

Sauqué V, Rabal-Garcés R, Sola-Almagro C, Cuenca-Bescós G (2014) Bone accumulation by leopards in the Late Pleistocene in the Moncayo Massif (Zaragoza, NE Spain). PLoS ONE 9:e92144. https://doi.org/10.1371/journal.pone.0092144

Sauqué V, Sanchis A, Madurell-Malapeira J (2018) Late Pleistocene leopards as a bone accumulator: taphonomic results from S'Espasa cave and other Iberian key sites. Hist Biol 30:821–834.

Serdyuk NV, Lavrov AV, Madurell-Malapeira J, Kemelman EL, Gimranov DO, Lopatin AV (2025) The resilience of an injured Early Pleistocene *Lynx* from Taurida cave (Crimea). Hist Biol 37:2379–2387. https://doi.org/10.1080/08912963.2024.2383711

Sunquist M, Sunquist F (2002) Wild cats of the world. University of Chicago Press, Chicago. https://doi.org/10.7208/chicago/9780226518237.001.0001

Van Valkenburgh B (2009) Costs of carnivory: tooth fracture in Pleistocene and Recent carnivorans. Biol J Linn Soc 96:68–81. https://doi.org/10.1111/j.1095-8312.2008.01108.x

Van Valkenburgh B, Hertel F (1993) Tough times at La Brea: tooth breakage in large carnivores of the Late Pleistocene. Science 261:456–459. https://doi.org/10.1126/science.261.5120.456

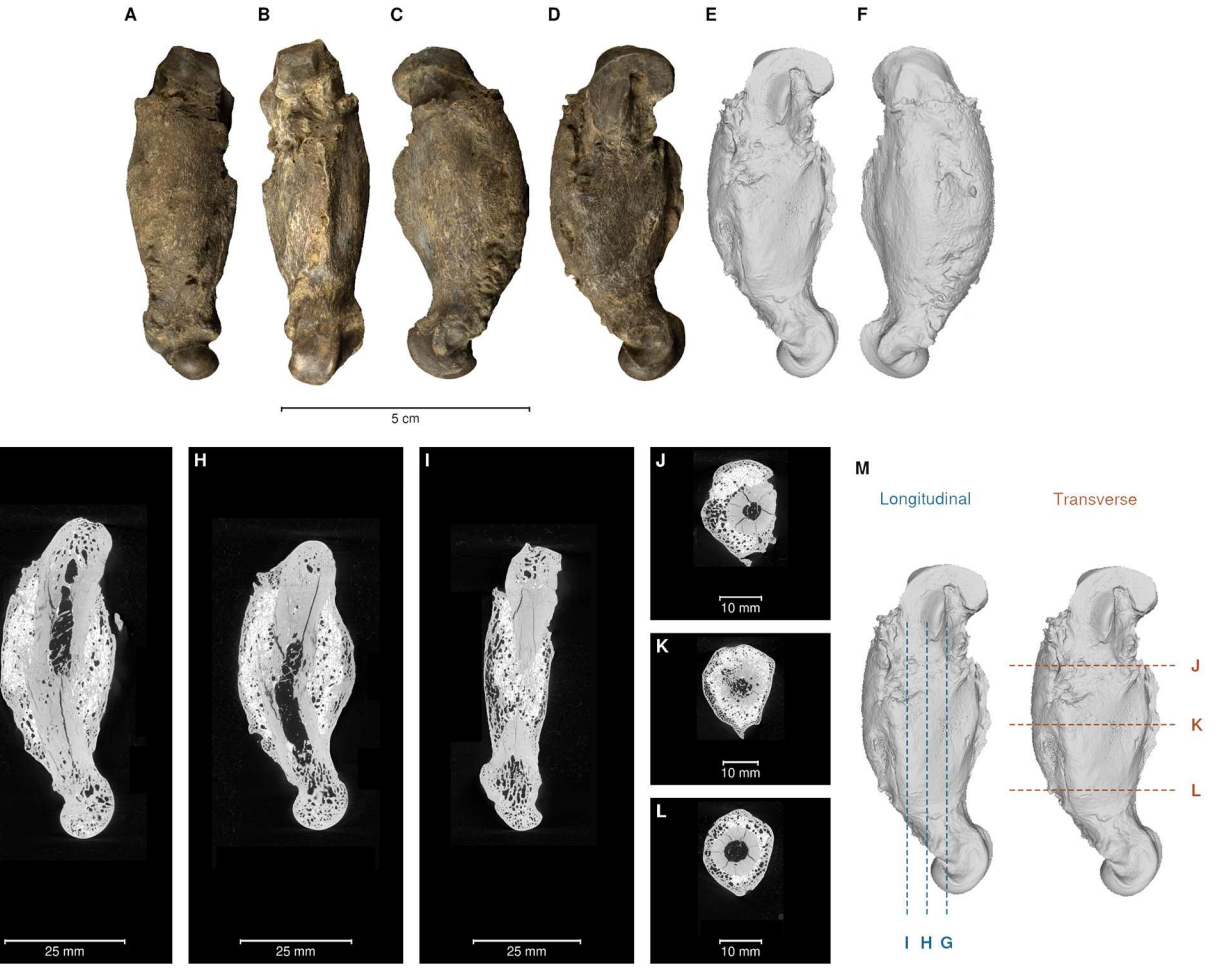
Figure captions

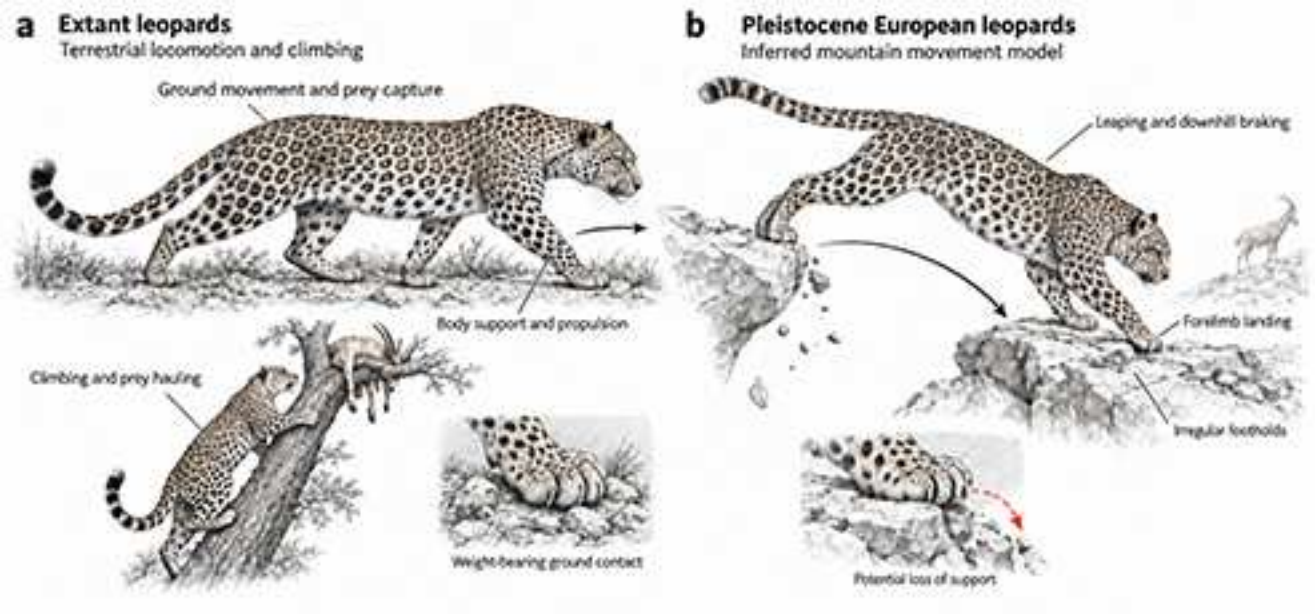
Fig. 1. Pathological right radius of *Panthera pardus* from Grotte de la Carrière, eastern French Pyrenees, layer 2 of Sondage 2 (GDC2021-S2-P30-624-Nv.2). **A, B**, lateral and medial views. **C, D,** three-dimensional surface representations in corresponding views. E, F, longitudinal computed-tomography sections through the affected shaft. **G, H**, transverse sections showing the expanded contour, reorganized bone and residual internal cavities. **I**, reference surface models indicating the approximate positions of longitudinal sections E and F (blue) and transverse sections G and H (orange).

Fig. 2 Pathological left fifth metacarpal of *Panthera pardus* from Tut de Fustanyà, eastern Catalan Pyrenees (RO25-834-Mg-03). **A–D**, anterior, posterior, lateral and medial views. **E, F**, three-dimensional surface representations of medial and lateral views. **G–I**, longitudinal computed-tomography sections showing altered cortical architecture, porous bone and an irregular medullary space. **J–L**, transverse sections through the shaft. **M**, reference surface models indicating the approximate positions of longitudinal sections G, H and I (blue) and transverse sections J, K and L (orange).

Fig. 3. Locomotor behaviour and proposed links between habitat use and traumatic fracture risk in extant and Pleistocene European leopards (*Panthera pardus*). **a**, Extant leopards combine terrestrial locomotion and prey capture with climbing and prey hauling, involving forelimb support, propulsion and weight-bearing contact. **b**, Inferred locomotor scenario for Pleistocene European leopards inhabiting steep, rocky terrain, illustrating leaping, downhill braking and forelimb landing on irregular footholds. Unstable substrates or an awkward landing could cause loss of support and expose the forelimb to abrupt, asymmetric loading. **c**, Proposed mechanical pathways linking contact stability to injury: stable contact allows controlled load transfer, whereas a misstep or failed landing may generate traumatic loading sufficient to cause a fracture. Red dashed arrows highlight loss of support and the potential progression to fracture.


A
B
C
D
5 cm
E
5 cm
F
5 cm
G
25 mm
H
25 mm
I
Longitudinal
Transverse
G
H
F
E


A
B
C
D
E
F
5 cm
G
H
I
J
K
L
25 mm
25 mm
25 mm
10 mm
10 mm
10 mm
M
Longitudinal
Transverse
J
K
L
I H G


a
Extant leopards
Terrestrial locomotion and climbing
Ground movement and prey capture
Body support and propulsion
Climbing and prey hauling
Weight-bearing ground contact
b
Pleistocene European leopards
Inferred mountain movement model
Leaping and downhill braking
Forelimb landing
Irregular footholds
Potential loss of support
c
Contact stability and traumatic loading
Stable contact
Controlled load transfer
No fracture expected
Misstep or failed landing
Abrupt asymmetric loading
Possible fracture