Received: 8 October 2025 | Accepted: 21 October 2025

DOI: 10.1002/ecs2.70542

ARTICLE

Ecosphere Naturalist

ECOSPHERE
AN ESA OPEN ACCESS JOURNAL

Opportunistic predation by carnivore mammals on females of pine processionary moths, *Thaumetopoea pityocampa*

Jacinto Román[1] | **Juan Carlos Rivilla**[1] | **Javier Calzada**[2] | **Francisco J. Palomares**[1]

[1]Department of Conservation Biology and Climate Change, Estación Biológica de Doñana-CSIC, Sevilla, Spain

[2]Departamento de Ciencias Integradas y Centro de Estudios Avanzados en Física, Matemáticas y Computación, Facultad de Ciencias Experimentales, Universidad de Huelva, Huelva, Spain

Correspondence
Jacinto Román
Email: jroman@ebd.csic.es

Funding information
Consejo Superior de Investigaciones Científicas, Grant/Award Number: PID2020-116571GB-I00

Handling Editor: Sunshine A. Van Bael

Abstract

The pine processionary moth (*Thaumetopoea pityocampa*, PPM) is a major defoliator in Mediterranean pine forests, with broad ecological and socioeconomic impacts. While vertebrate predators of its eggs, larvae, pupae, and imagos have been well documented, predation on adult females by mammals has not been previously described. Here, we present the first evidence of opportunistic predation by generalist carnivores on PPM imago females. We collected and analyzed fecal samples of red foxes (*Vulpes vulpes*), stone martens (*Martes foina*), common genets (*Genetta genetta*), and European badgers (*Meles meles*) in several Spanish mountain ranges between 2022 and 2024. Morphological and molecular analyses revealed PPM eggs and anal scales in 19.1% of red fox and 11.3% of stone marten feces in Cazorla in 2022, with mean counts of 1773 and 680 eggs per feces, respectively. This predation likely results from the limited dispersal and ground activity of ovipositing females, making them accessible prey for opportunistic terrestrial carnivores. Further studies are needed to assess the frequency, spatial extent, and ecological significance of this phenomenon, as well as its potential role in integrated pest management strategies.

KEYWORDS
biological control, ecological surprise, forestry, pests, plague, red fox, stone marten

Insect populations susceptible to pest outbreaks are regulated by natural enemies, including predators, parasitoids, and pathogens, which help maintain ecological balance (Dwyer et al., 2004; Elkinton et al., 1996; Janssen & van Rijn, 2021). In recent silvicultural practices, promoting natural predator populations is a widely used method for biological control of pest outbreaks (de Boer & Harvey, 2020; Klapwijk et al., 2016; Plat et al., 2025). Yet, effective implementation requires a detailed understanding of which species prey on each pest and the stages of the pest's life cycle they target.

The pine processionary moth (*Thaumetopoea pityocampa*; hereafter PPM) is an oligophagous moth of the Mediterranean region, which feeds on conifers of the genus *Pinus* and *Cedrus*, with economic, medical, and conservation concerns (Bonamonte et al., 2013; CABI, 2025; Gatto et al., 2009; Hódar et al., 2003; Hodar & Zamora, 2004). The vertebrate predators of the PPM are well documented, with distinct species targeting specific

developmental stages (Battisti et al., 2015; de Boer & Harvey, 2020). Eggs that are laid in batches on pine needles are consumed by some birds, such as tits (Barbaro & Battisti, 2011). From the third instar onwards, caterpillars develop urticating setae, which serve as a defense mechanism against vertebrate predators. However, some species have evolved specific techniques and adaptations that allow them to feed on these larvae (Battisti et al., 2015). For instance, tits consume only the internal tissues of the caterpillars, avoiding the urticating setae, while cuckoos (*Clamator glandarius* and *Cuculus canorus*) possess gizzards adapted to expel the setae through regurgitation (Barbaro & Battisti, 2011; Gonzalez-Cano, 1981). At the end of their development, larvae make a head-to-tail procession occurring most commonly from late winter to spring and look for favorable places to bury themselves in the ground (Dulaurent et al., 2011; Samalens & Rossi, 2011). Once pupated in the soil, there is high predation pressure, particularly from hoopoe (*Upupa epops*), whose long, curved bill is especially adapted to access this subterranean life stage (Barbaro et al., 2008; Battisti et al., 2000). Wild boars (*Sus scrofa*) also prey on the pupae, digging them out through rooting behavior (Battisti et al., 2015). The seasonal flight activity of the imagos typically lasts from 2 to 4 months during the summer and are eaten in flight by nocturnal aerial hunters, such as nightjars, *Caprimulgus* sp., and bats (Augusto et al., 2024; Battisti et al., 2015; Garin et al., 2019). Male moths exhibit more frequent flight activity while actively searching for mates (CABI, 2025; Charbonnier et al., 2014; Démolin, 1969; Garin et al., 2019; Mirchev et al., 2013; Zhang & Paiva, 1998), making them more exposed and, therefore, more likely to be targeted by these predators. In contrast, females are less exposed to aerial predators because they live only 1–2 days and exhibit limited flight and dispersal capacity, typically ovipositing on nearby pines (Battisti et al., 2015; CABI, 2025; Devkota et al., 1992; Zhang & Paiva, 1998), although some individuals can travel up to a few kilometers (Démolin, 1969).

Here, we document a previously undescribed predation pattern on PPM imago females by generalist, carnivore mammals.

As part of a wide project to study the trophic relationships among carnivore mammals, feces were collected from four species of generalist carnivores: red fox, *Vulpes vulpes*; stone marten, *Martes foina*; common genet, *Genetta genetta*; and badger, *Meles meles*. The feces of common genets and European badgers were readily identifiable to species level due to their distinctive morphology and characteristic deposition in latrines (Blanco-Garrido & Rivas, 2014; Salgado, 2014). In contrast, feces from red foxes and stone martens are more difficult to distinguish from one another or from those of other species such as domestic dogs; therefore, species identification was performed using molecular analyses (see below). Only freshest feces were collected to ensure that the samples represented the summer period.

Feces were collected at a distance of less than 1500 m from pine forests between the end of June and the beginning of July 2022 and 2023, in Sierras de Cazorla, Segura y Las Villas (hereafter Cazorla; 2000 km^2), and Sierra de Aracena (1870 km^2), and in 2023 in Sierra Nevada (1720 km^2) (Figure 1). Cazorla and Sierra Nevada have large areas of pine forests, and Sierra de Aracena has only small areas planted with pine trees. In September 2024, red fox, stone marten, and/or common genet feces were searched again in Cazorla, Sierra Nevada, and in a new area, Cartaya, an area with a pine extension of 5700 ha (Figure 1). In these extra samplings, we did not identify species by molecular analyses, since we were only interested in checking the presence of predation of PPM imago females in generalist carnivores. Feces were identified to species level by the researchers using prior experience, based on morphological characteristics and the deposition site.

For molecular analyses, we hydrated the surface of the feces with a preservative solution (buffer), and a swab moistened with the same buffer was rubbed on the surface of the excrement and stored in an Eppendorf tube with the same buffer. The collected feces were stored in paper bags with silica gel and then dried in an oven at 60°C inside a fume hood.

DNA extraction was performed in the Molecular Ecology Laboratory (LEM) at the Doñana Biological Station (EBD) under sterile conditions. A two-step procedure was applied to the swabs collected in the field, consisting of digestion and extraction, following the typical methodology for degraded, scarce, and old samples (Boom et al., 1990; Höss & Pääbo, 1993).

On the DNA extraction, we first used specific primers that amplify conserved regions of the mitochondrial cytochrome b gene in several Iberian species (Fernandes et al., 2008). These regions are easily distinguishable between species due to size differences observed through agarose gel electrophoresis.

The analysis of the excrement content was performed by manual techniques, which consisted of breaking up samples into separate micro and macro-remains of prey, followed by their identification using reference collections (Putman, 1984; Reynolds & Aebischer, 1991).

Fecal examinations revealed characteristic white dots in some samples, which were later identified as PPM eggs approximately 1 mm in diameter (Figure 2D). Laboratory analyses also detected PPM anal scales (Figure 2F), which appeared rolled up due to passage through the

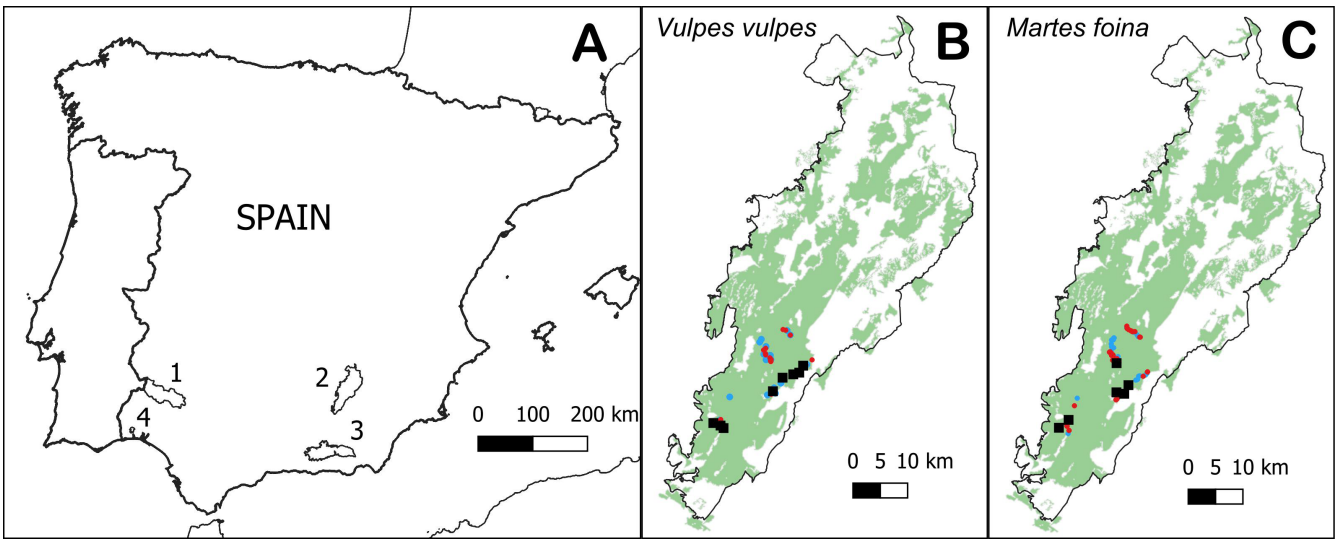

FIGURE 1 (A) Location of the survey areas in the Iberian Peninsula: (1) Sierra de Aracena Natural Park; (2) Cazorla, Segura y Las Villas Natural Park; (3) Sierra Nevada Natural Park; and (4) Cartaya pine forest. (B, C) Detail of the Cazorla, Segura y Las Villas Natural Park. The green area indicates the distribution of the pine forest areas; the blue dots indicate the feces collected in 2022, and the red ones in 2023; the black squares indicate the location of the excrements in which the remains of imago females of the processionary pine moth were found.

digestive tract of the carnivores (Figure 2E). These scales are characteristic and diagnostic of each species of *Thaumetopoea* (Agenjo, 1941; Frerot & Demolin, 1993).

Table 1 summarizes the total number of fecal samples by predator, year, study area, and the count containing PPM eggs and/or scales. PPM eggs and scales were detected in the feces of red foxes (19.1%; $n = 42$) and stone martens (11.3%; $n = 53$) in the Cazorla area in 2022, but not in those of genets and badgers. No occurrences were found in 2023. In 2024, only suspected PPM-positive feces were collected (see Figure 2D). PPM eggs and scales were found in four feces, likely from red fox in Cazorla.

To estimate the number of PPM eggs present in each excrement, the contents were homogenized, and the number of eggs was counted in a quarter and extrapolated to the total. A mean of 1773 (SD = 1054; range: 420–3500; $n = 8$) eggs were found in red fox feces, and 680 (SD = 1032; range: 20–2400; $n = 6$) in stone marten feces.

The maximum distance between excrements with PPM eggs was 19 km for red foxes and 16 km for stone martens. These values greatly exceed the home range of both species (Abramov, 2024; Soulsbury & Statham, 2023), so it can be ensured that the excrements belonged to different individuals.

Based on the frequency of occurrence and the average number of eggs per excrement, it is possible to estimate the consumption of females of PPM by red foxes and stone martens in 2022 in our study area in Cazorla. To do this conservatively, we used the minimum density for foxes and stone martens found in Spain, which is 0.3 individuals/km^2 (Abramov, 2024; Jimenez et al., 2019; Jiménez et al., 2017; Rau et al., 1985; Sarmento et al., 2009). The defecation rate described in different studies for the red fox ranges between 4.4 and 9.4 defecations per day (Ferreras & Fernandez-de-Simon, 2019; Webbon et al., 2004). For the stone marten, no studies have been conducted, but for the pine marten, *Martes martes*, a species ecologically and morphologically similar, the defecation rate is between 5 and 15 defecations per day (Birks et al., 2005; Caryl et al., 2012). Using the lower values of defecations per day for the red fox and the stone marten, during the two months (60 days) in which the main flight period of PPM occurs, each species would have produced 79.2 and 90 feces/km^2, respectively. Based on our data, these would contain an estimated 26,821 PPM eggs/km^2 in red fox feces and 6916 PPM eggs/km^2 in stone marten feces. Since female PPM in the Iberian Peninsula carry on average 200 eggs (Schmidt et al., 2001), red foxes and stone martens would have consumed at least 134 and 35 females of PPM/km^2, respectively.

Although the presence of Lepidoptera caterpillars is habitual in the diet of non-flying mammals, such as rodents, monkeys, or carnivores (Bryer et al., 2015; Elkinton et al., 1996; Ménard, 1984; Pigozzi, 1991), cases of imago predation are rare and have been described for vulnerable situations, such as predation of overwintering adults of butterflies by rodents (Brower et al., 1985; Wiklund et al., 2008). To our knowledge, there are no

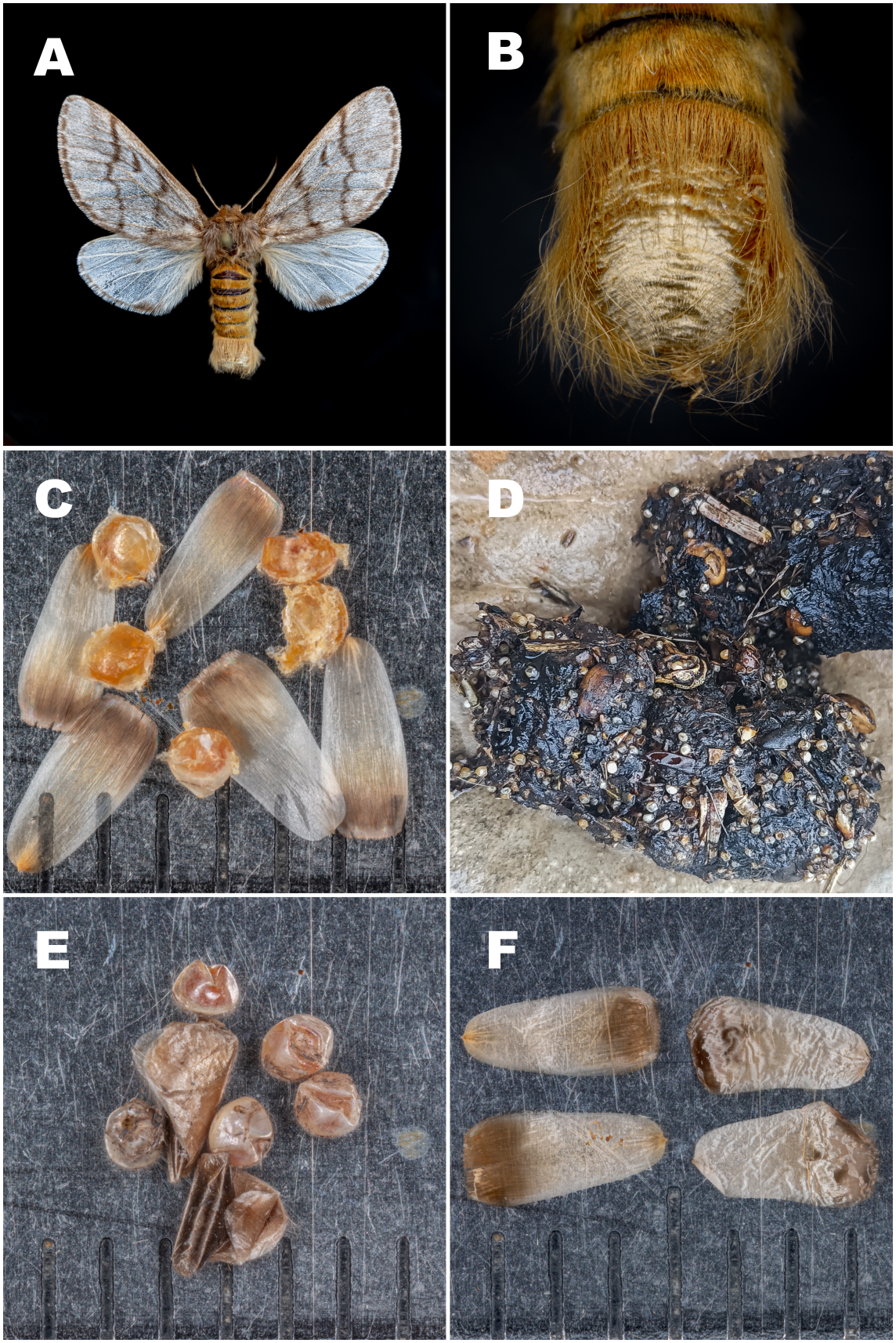

FIGURE 2 Legend on next page.

TABLE 1 Number of feces of each carnivore mammal collected in or close to pine forest of several study areas of the Iberian Peninsula.

Year	*Vulpes vulpes*	*Martes foina*	*Meles meles*	*Genetta genetta*
Cazorla_2022	42 (8)	53 (6)	11	37
Cazorla_2023	27	50	5	10
Nevada_2023	40	31	16	51
Aracena_2022	5	8	...	6
Aracena_2023	2	...	...	...
Cazorla_2024	264 (4)	110	...	...
Nevada_2024	236	22	...	70
Cartaya_2024	107	...	...	...

Note: Only feces collected closer than 1500 m from a pine forest were considered. In parentheses, the number of feces containing pine processionary moth eggs. In the 2022 and 2023 sampling, red fox and stone marten feces were identified genetically. In the extra sampling of 2024, only red fox, stone marten, and/or common genet feces were searched for and were not identified genetically, although based on the experience of the two previous years, we assigned them to a carnivore species. In addition, during 2024, sampling only feces that externally appeared to have pine processionary moth (PPM) eggs, such as those in Figure 2D, was collected. Cazorla: Sierras de Cazorla, Segura y las Villas; Nevada: Sierra Nevada; Aracena: Sierra de Aracena; Cartaya, extra locality survey only in 2024.

previous records of moth predation by carnivorous mammals.

Here, we report the first evidence of predation on female moths by generalist carnivores. Accessibility to this prey is undoubtedly facilitated by the reduced movement ability of these imago females (CABI, 2025; Devkota et al., 1992); indeed, we have observed imago females walking on the pine forest floor at dawn. This appears to be an opportunistic form of predation, dependent on local availability, which is already reflected in the variation observed in our dataset. However, more studies would be necessary to assess the generality of the phenomenon described here. The traditional view of how generalist predators (mainly mammals) affect forest lepidopteran pests suggests that they only control prey at low densities (see, e.g., Gschwantner et al., 2002; Liebhold et al., 1998), which does not seem to be our case of opportunistic predation. However, predation on imago females of PPM could be a key factor in the biological control of the species (CABI, 2025). It seems logical that consuming a female full of eggs would have a greater impact on the population than eating caterpillars, pupae, or male moths individually, as other predators do (Battisti et al., 2015). Nonetheless, conclusions about this effect cannot be drawn without first knowing the PPM population levels.

Although we have not found predation by common genets or badgers in our preliminary study, this cannot be completely ruled out, as well as that of other opportunistic mammals. Both species consume a wide variety of invertebrates (Gaubert et al., 2024; Newman & Buesching, 2024), and their presence in pine-dominated habitats during the PPM flight period suggests that they might occasionally prey on females, particularly under conditions of high local abundance or reduced prey availability. Future studies using molecular identification can help determine if more species of terrestrial mammals prey on PPM females.

Our results highlight once again the importance of the conservation of complex and well-structured communities in which the presence of generalist predators is a key element in the control of species that can develop into pests (Dupuy et al., 2009; Symondson et al., 2002; Wyckhuys et al., 2024).

AUTHOR CONTRIBUTIONS

Jacinto Román, Javier Calzada, and Francisco J. Palomares conceptualized the study. Jacinto Román, Javier Calzada, Juan Carlos Rivilla, and Francisco J. Palomares collected the samples. Juan Carlos Rivilla performed the dietary analysis. Jacinto Román drafted the original manuscript. All authors revised and approved the final version of the manuscript. Francisco J. Palomares secured funding for the study.

FIGURE 2 (A) Imago female of processionary pine moth. (B) Detail of the anal scales used by the female to protect the eggs, in the tip of the abdomen. (C) Detail of the scales and eggs extracted from a collection specimen. (D) Red fox excrement showing the pine processionary eggs on the surface. (E) Eggs and scales extracted from a red fox excrement; the scales are grouped and rolled up due to passage through the carnivore's digestive tract. (F) Comparison of anal scales extracted from a collection specimen (left) and from an excrement (right), once stretched. Photo credit: Jacinto Román.

ACKNOWLEDGMENTS

During the fieldwork, we received support from Miguel Ángel Castillo and David Cuerda, ranger and conservation technician of the Natural Park of Cazorla, Segura y Las Villas, respectively. Fernando Jubete provided us with moth specimens from his collection for the study. Irene Quintanilla performed the genetic analysis. Gloria López Pantoja advised us on the biology of PPM and provided information on pine forest infestation levels, which was used to design some of the sampling transects in 2024. The collection of the samples had the permission of the Junta de Andalucía. The Doñana Biological Station provided us with its facilities at the Roblehondo house in the Sierra de Cazorla, Segura y Las Villas. This study was funded by the SETROCAR Project PID2020-116571GB-I00, which was financed by the Spanish Ministry of Science and Innovation.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Palomares et al., 2025) are available from the Digital CSIC Repository: https://doi.org/10.20350/digitalCSIC/17650.

ORCID

Jacinto Román https://orcid.org/0000-0003-0675-9432
Francisco J. Palomares https://orcid.org/0000-0002-4655-7205

REFERENCES

Abramov, A. V. 2024. "Stone Marten *Martes foina* (Erxleben, 1777)." In *Handbook of the Mammals of Europe*, Vol. 22, edited by K. Hackländer and F. E. Zachos, 1–22. Cham: Springer International Publishing. https://doi.org/10.1007/978-3-319-65038-8_128-1.

Agenjo, R. 1941. "Monografía de la familia Thaumetopoeidae (Lep.)." *Eos* 17: 69–130.

Augusto, A. M., H. Raposeira, P. Horta, V. A. Mata, O. Aizpurua, A. Alberdi, G. Jones, et al. 2024. "Bat Diversity Boosts Ecosystem Services: Evidence from Pine Processionary Moth Predation." *Science of the Total Environment* 912: 169387. https://doi.org/10.1016/j.scitotenv.2023.169387.

Barbaro, L., and A. Battisti. 2011. "Birds as Predators of the Pine Processionary Moth (Lepidoptera: Notodontidae)." *Biological Control* 56(2): 107–114. https://doi.org/10.1016/j.biocontrol.2010.10.009.

Barbaro, L., L. Couzi, V. Bretagnolle, J. Nezan, and F. Vetillard. 2008. "Multi-Scale Hábitat Selection and Foraging Ecology of the Eurasian Hoopoe (*Upupa epops*) in Pine Plantations." *Biodiversity and Conservation* 17: 1073–87. https://doi.org/10.1007/s10531-007-9241-z.

Battisti, A., M. Avci, D. N. Avtzis, M. L. Ben Jamaa, L. Bernardi, W. Berretima, M. Branco, et al. 2015. "Natural History of the Processionary Moths (*Thaumetopoea* Spp.): New Insights in Relation to Climate Change." In *Processionary Moths and Climate Change: An Update*, edited by A. Roque, 15–79. Dordrecht: Springer. https://doi.org/10.1007/978-94-017-9340-7.

Battisti, A., M. Bernardi, and C. Ghiraldo. 2000. "Predation by the Hoopoe on Pupae of *Thaumetopoea pityocampa* and the Likely Influence on Other Natural Enemies." *BioControl* 45: 311–323. https://doi.org/10.1023/A:1009992321465.

Birks, J., J. Messenger, T. Braithwaite, A. Davison, R. Brookes, and C. Strachan. 2005. "Are Scat Surveys a Reliable Method for Assessing Distribution and Population Status of Pine Martens?" In *Martens and Fishers (Martes) in Human-Altered Environments*, edited by D. J. Harrison, A. K. Fuller, and G. Proulx, 235–252. Boston, MA: Springer. https://doi.org/10.1007/0-387-22691-5_12.

Blanco-Garrido, F., and A. Rivas. 2014. "Gineta *Genetta genetta* (Linnaeus, 1758)." In *Guía virtual de los indicios de los mamíferos de la Península Ibérica, Islas Baleares y Canarias*, edited by J. Calzada, M. Clavero, and A. Fernández, 1–6. Sevilla: Sociedad Española para la Conservación y Estudio de los Mamíferos (SECEM).

Bonamonte, D., C. Foti, M. Vestita, and G. Angelini. 2013. "Skin Reactions to Pine Processionary Caterpillar *Thaumetopoea pityocampa* Schiff." *The Scientific World Journal* 2013: 867431. https://doi.org/10.1155/2013/867431.

Boom, R., C. J. A. Sol, M. M. M. Salimans, C. L. Jansen, P. M. E. van Wertheim-Dillen, and J. van der Noordaa. 1990. "Rapid and Simple Method for Purification of Nucleic Acids." *Journal of Clinical Microbiology* 28: 495–503. https://doi.org/10.1128/jcm.28.3.495-503.1990.

Brower, L. P., B. E. Horner, M. A. Marty, C. M. Moffitt, and B. Villa-R. 1985. "Mice (*Peromyscus maniculatus*, *P. spicilegus*, and *Microtus mexicanus*) as Predators of Overwintering Monarch Butterflies (*Danaus plexippus*) in Mexico." *Biotropica* 17(2): 89–99. https://doi.org/10.2307/2388500.

Bryer, M. A. H., C. A. Chapman, D. Raubenheimer, J. E. Lambert, and J. M. Rothman. 2015. "Macronutrient and Energy Contributions of Insects to the Diet of a Frugivorous Monkey (*Cercopithecus ascanius*)." *International Journal of Primatology* 36: 839–854. https://doi.org/10.1007/s10764-015-9857-x.

CABI. 2025. "*Thaumetopoea pityocampa* (Pine Processionary)." In *CABI Compendium*. Wallingford: CAB International. https://doi.org/10.1079/cabicompendium.53501.

Caryl, F. M., R. Raynor, C. P. Quine, and K. J. Park. 2012. "British Martens Are Facultative Trophic Specialists." *Journal of Zoology* 288: 252–59. https://doi.org/10.1111/j.1469-7998.2012.00951.x.

Charbonnier, Y., L. Barbaro, A. Theillout, and H. Jactel. 2014. "Numerical and Functional Responses of Forest Bats to a Major Insect Pest in Pine Plantations." *PLoS One* 9(10): e109488. https://doi.org/10.1371/journal.pone.0109488.

de Boer, J. G., and J. A. Harvey. 2020. "Range-Expansion in Processionary Moths and Biological Control." *Insects* 11: 267. https://doi.org/10.3390/insects11050267.

Démolin, G. 1969. "Comportement des adultes de *Thaumetopoea pityocampa* Schiff. Dispersion spatiale, importance écologique." *Annales des Sciences Forestières* 26(1): 81–102. https://doi.org/10.1051/forest/19690104.

Devkota, B., M. Breuer, and G. H. Schmidt. 1992. "Observations on the Flight Activity of the Pine Processionary Moth *Thaumetopoea pityocampa* (Den. & Schiff.) in Greece, Using synthetìc Sex-Pheromone and Light Traps (Insecta Lepidoptera Thaumetopoeidae)." *Bollettino di Zoologia Agraria e di Bachicoltura, Serie II* 24(2): 147–157.

Dulaurent, A. M., A. J. Porté, I. Van Halder, F. Vetillard, P. Menassieu, and H. Jactel. 2011. "A Case of Habitat Complementation in Forest Pests: Pine Processionary Moth Pupae Survive Better in Open Areas." *Forest Ecology and Management* 261: 1069–76. https://doi.org/10.1016/j.foreco.2010.12.029.

Dupuy, G., P. Giraudoux, and P. Delattre. 2009. "Numerical and Dietary Responses of a Predator Community in a Temperate Zone of Europe." *Ecography* 32: 277–290. https://doi.org/10.1111/j.1600-0587.2008.04930.x.

Dwyer, G., J. Dushoff, and S. H. Yee. 2004. "The Combined Effects of Pathogens and Predators on Insect Outbreaks." *Nature* 430: 341–45. https://doi.org/10.1038/nature02569.

Elkinton, J. S., W. M. Healy, J. P. Buonaccorsi, G. H. Boettner, A. M. Hazzard, H. R. Smith, and A. M. Liebhold. 1996. "Interactions among Gypsy Moths, White-Footed Mice, and Acorns." *Ecology* 77(8): 2332–42. https://doi.org/10.2307/2265735.

Fernandes, C. A., C. Ginja, I. Pereira, R. Tenreiro, M. W. Bruford, and M. Santos-Reis. 2008. "Species-Specific Mitochondrial DNA Markers for Identification of Non-Invasive Samples from Sympatric Carnivores in the Iberian Peninsula." *Conservation Genetics* 9: 681–690. https://doi.org/10.1007/s10592-007-9364-5.

Ferreras, P., and J. Fernandez-de-Simon. 2019. "Correction Factors for Estimating Food Consumption by Red Fox *Vulpes vulpes* from Scats." *Wildlife Biology* 2019: 1–9. https://doi.org/10.2981/wlb.00557.

Frerot, B., and G. Demolin. 1993. "Sex Pheromone of the Processionary Moths and Biosystematic Considerations within the Genus *Thaumetopoea* (Thaumetopoeidae Thaumetopoeinae)." *Bollettino di Zoologia Agraria e di Bachicoltura, Serie II* 25(1): 33–40.

Garin, I., J. Aihartza, U. Goiti, A. Arrizabalaga-Escudero, J. Nogueras, and C. Ibáñez. 2019. "Bats from Different Foraging Guilds Prey upon the Pine Processionary Moth." *PeerJ* 7: e7169. https://doi.org/10.7717/peerj.7169.

Gatto, P., A. Zocca, A. Battisti, M. J. Barrento, M. Branco, and M. R. Paiva. 2009. "Economic Assessment of Managing Processionary Moth in Pine Forests: A Case-Study in Portugal." *Journal of Environmental Management* 90(2): 683–691. https://doi.org/10.1016/j.jenvman.2008.01.007.

Gaubert, P., C. Nores, D. Camps, and E. Do Linh San. 2024. "Common Genet *Genetta genetta* (Linnaeus, 1758)." In *Handbook of the Mammals of Europe*, Vol. 28, edited by K. Hackländer and F. E. Zachos, 1–28. Cham: Springer International Publishing. https://doi.org/10.1007/978-3-319-65038-8_149-1.

Gonzalez-Cano, J. M. 1981. "Predacion de procesionaria del pino por vertebrados en la zona de Mora de Rubielos (Teruel)." *Boletín de la Estación Central de Ecología* 10: 53–77.

Gschwantner, T., G. Hoch, and A. Schopf. 2002. "Impact of Predators on Artificially Augmented Populations of *Lymantria dispar* L. Pupae (Lep., Lymantriidae)." *Journal of Applied Entomology* 126: 66–73. https://doi.org/10.1046/j.1439-0418.2002.00626.x.

Hódar, J. A., J. Castro, and R. Zamora. 2003. "Pine Processionary Caterpillar *Thaumetopoea pityocampa* as a New Threat for Relict Mediterranean Scots Pine Forests under Climatic Warming." *Biological Conservation* 110(1): 123–29. https://doi.org/10.1016/S0006-3207(02)00183-0.

Hodar, J. A., and R. Zamora. 2004. "Herbivory and Climatic Warming: A Mediterranean Outbreaking Caterpillar Attacks a Relict, Boreal Pine Species." *Biodiversity and Conservation* 13: 493–500. https://doi.org/10.1023/B:BIOC.0000009495.95589.a7.

Höss, M., and S. Pääbo. 1993. "DNA Extraction from Pleistocene Bones by a Silica-Based Purification Method." *Nucleic Acids Research* 21(16): 3913–14. https://doi.org/10.1093/nar/21.16.3913.

Janssen, A., and P. C. J. van Rijn. 2021. "Pesticides Do Not Significantly Reduce Arthropod Pest Densities in the Presence of Natural Enemies." *Ecology Letters* 24(9): 2010–24. https://doi.org/10.1111/ele.13819.

Jimenez, J., R. Chandler, J. Tobajas, E. Descalzo, R. Mateo, and P. Ferreras. 2019. "Generalized Spatial Mark–Resight Models with Incomplete Identification: An Application to Red Fox Density Estimates." *Ecology and Evolution* 9: 4739–48. https://doi.org/10.1002/ece3.5077.

Jiménez, J., J. Nuñez-Arjona, C. Rueda, L. M. González, F. García-González, J. Muñoz-Igualada, and J. V. López-Bao. 2017. "Estimating Carnivore Community Structures." *Scientific Reports* 7: 41036. https://doi.org/10.1038/srep41036.

Klapwijk, M. J., H. Bylund, M. Schroeder, and C. Björkman. 2016. "Forest Management and Natural Biocontrol of Insect Pests." *Forestry* 89(3): 253–262. https://doi.org/10.1093/forestry/cpw019.

Liebhold, A. M., Y. Higashiura, and A. Unno. 1998. "Forest Type Affects Predation on Gypsy Moth (Lepidoptera: Lymantriidae) Pupae in Japan." *Environmental Entomology* 27: 858–862. https://doi.org/10.1093/ee/27.4.858.

Ménard, N. 1984. "Le régime alimentaire de *Macaca sylvanus* dans différents habitats d'Algérie. 1. -Régime en chênaie décidue." *Revue d'Écologie* 40(4): 451–466.

Mirchev, P., G. Georgiev, and G. Geshev. 2013. "Dispersal of Male Butterflies of Pine Processionary Moth (*Thaumetopoea pityocampa*)." *Silva Balcanica* 14(1): 102–8.

Newman, C., and C. D. Buesching. 2024. "European Badger *Meles meles* (Linnaeus, 1758)." In *Handbook of the Mammals of Europe*, edited by K. Hackländer and F. E. Zachos, 1–27. Cham: Springer Nature Switzerland. https://doi.org/10.1007/978-3-319-65038-8_131-1.

Palomares, F., J. C. Rivilla, J. Calzada, J. Román, and J. A. Alguazas Martínez. 2025. "Collected_Carnivore_Scats_SETROCAR.xlsx." Dataset. DIGITAL.CSIC. https://doi.org/10.20350/digitalCSIC/17650.

Pigozzi, G. 1991. "The Diet of the European Badger in a Mediterranean Coastal área." *Acta Theriologica* 36(3–4): 293–306. https://doi.org/10.4098/AT.arch.91-31.

Plat, N., L. Moreews, L. Schillé, J.-B. Rivoal, and H. Jactel. 2025. "Conservation Biological Control in Forest: A Case Study with the Pine Processionary Moth." *Biological Control* 202: 105702. https://doi.org/10.1016/j.biocontrol.2025.105702.

Putman, R. J. 1984. "Facts from Faeces." *Mammal Review* 14: 79–97. https://doi.org/10.1111/j.1365-2907.1984.tb00341.x.

Rau, J. R., J. F. Beltrán, and M. Delibes. 1985. "Can the Increase of Fox Density Explain the Decrease in Lynx Numbers at Doñana?" *Revue d'Écologie (La Terre et la Vie)* 40: 145–150.

Reynolds, J. C., and N. J. Aebischer. 1991. "Comparison and Quantification of Carnivore Diet by Faecal Analysis: A Critique, with Recommendations, Based on a Study of the Fox *Vulpes vulpes*." *Mammal Review* 21: 97–122. https://doi.org/10.1111/j.1365-2907.1991.tb00113.x.

Salgado, I. 2014. "Tejón europeo *Meles meles* (Linnaeus, 1758)." In *Guía virtual de los indicios de los mamíferos de la Península Ibérica, Islas Baleares y Canarias*, edited by J. Calzada, M. Clavero, and A. Fernández, 1–8. Sevilla: Sociedad Española para la Conservación y Estudio de los Mamíferos (SECEM).

Samalens, J. C., and J. P. Rossi. 2011. "Does Landscape Composition Alter the Spatiotemporal Distribution of the Pine Processionary Moth in a Pine Plantation Forest?" *Population Ecology* 53: 287–296. https://doi.org/10.1007/s10144-010-0227-4.

Sarmento, P., J. Cruz, C. Eira, and C. Fonseca. 2009. "Evaluation of Camera Trapping for Estimating Red Fox Abundance." *The Journal of Wildlife Management* 73: 1207–12. https://doi.org/10.2193/2008-288.

Schmidt, G. H., E. Tanzen, and S. Bellin. 2001. "Structure of Egg-Batches of *Thaumetopoea pityocampa* (Den. And Schiff.) (Lep., Thaumetopoeidae), Egg Parasitoids and Rate of Egg Parasitism on the Iberian Peninsula." *Journal of Applied Entomology* 123: 449–458. https://doi.org/10.1046/j.1439-0418.1999.00405.x.

Soulsbury, C. D., and M. J. Statham. 2023. "Red fox *Vulpes vulpes* (Linnaeus, 1758)." In *Handbook of the Mammals of Europe*, edited by K. Hackländer and F. E. Zachos, 1–26. Cham: Springer International Publishing. https://doi.org/10.1007/978-3-319-65038-8_119-1.

Symondson, W. O. C., K. D. Sunderland, and M. H. Greenstone. 2002. "Can Generalist Predators be Effective Biocontrol Agents?" *Annual Review of Entomology* 47: 561–594. https://doi.org/10.1146/annurev.ento.47.091201.145240.

Webbon, C. C., P. J. Baker, and S. Harris. 2004. "Faecal Density Counts for Monitoring Changes in Red Fox Numbers in Rural Britain." *Journal of Applied Ecology* 41: 768–779. https://doi.org/10.1111/j.0021-8901.2004.00930.x.

Wiklund, C., A. Vallin, M. Friberg, and S. Jakobsson. 2008. "Rodent Predation on Hibernating Peacock and Small Tortoiseshell Butterflies." *Behavioral Ecology and Sociobiology* 62: 379–389. https://doi.org/10.1007/s00265-007-0465-4.

Wyckhuys, K. A. G., G. Pozsgai, I. B. Fekih, F. J. Sánchez-García, and M. Elkahky. 2024. "Biodiversity Loss Impacts Top-Down Regulation of Insect Herbivores across Ecosystem Boundaries." *Science of the Total Environment* 930: 172807. https://doi.org/10.1016/j.scitotenv.2024.172807.

Zhang, Q. H., and M. R. Paiva. 1998. "Female Calling Behaviour and Male Response to the Sex Pheromone in *Thaumetopoea pityocampa* (Den. And Schiff.) (Lep., Thaumetopoeidae)." *Journal of Applied Entomology* 122: 353–360. https://doi.org/10.1111/j.1439-0418.1998.tb01512.x.

How to cite this article: Román, Jacinto, Juan Carlos Rivilla, Javier Calzada, and Francisco J. Palomares. 2026. "Opportunistic Predation by Carnivore Mammals on Females of Pine Processionary Moths, *Thaumetopoea Pityocampa*." *Ecosphere* 17(2): e70542. https://doi.org/10.1002/ecs2.70542