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The secret life of a rock-dweller: arboreal acrobatics observed in the European leaf-toed gecko *Euleptes europaea*

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Abstract

The European leaf toed Gecko, *Euleptes europaea*, is a strictly nocturnal species endemic to the western Mediterranean and has long been considered a rock-specialist as it is associated with this habitat during its entire daily and life cycle. In this study, we report observations of arboreal behaviour in *E. europaea*, collected during field research over a 40-year period from across the entire species range. We provide a review of the available information on this topic that contributes to a refined view of the habitat uses and arboreal abilities of this species. Arboreal behaviour in *E. europaea* was observed throughout the year, across different macrohabitats, on a wide variety of tree, shrub, and bush species, on various parts of the plant (trunk, branches, fronds, twigs, leaves), and at different height from the ground. Remarkably, *E. europaea* shows an extraordinarily agile arboreal locomotion associated with striking morphological adaptations to an arboreal lifestyle, namely a prehensile tail bearing a terminal adhesive pad that supplements grasping force, an equilibrium asset, and scansor adhesion both in static condition and during escape. We conclude that *E. europaea* is a climbing gecko (opposed to ground dwelling), occupying both rocky and arboreal microhabitats. While the evolutionary origin and ecological drivers of the arboreal behaviour of *E. europaea* remains to be fully investigated, this realization has important implications for designing fieldwork research and management strategies for conservation.

Key Words

arboreal behaviour, Gekkota, microhabitat use, prehensile tail, rock crevices, tail pads, vegetation cover

Introduction

Understanding the habitat use of species is crucial for ecologists, biogeographers, and conservationists (MacArthur and Pianka 1966; Caughley 1994; Hanski and Gyllenberg 1997). Species differ greatly in the range of habitat they use. Some species are habitat generalists while others are specialists, with a gradient of variation between the two extremes. Habitat selection is particularly important for ectothermic lizards such as geckos, because it influences thermal ecology, physiological performance, and individual behaviour, thus having an impact upon population and community dynamics (Pulliam and Danielson 1991; Pandit et al. 2009). However, for many species, we still have a very limited knowledge of their habitat use.

Here, we report original observations and literature data on the European leaf toed Gecko *Euleptes europaea* that warrant a reconsideration of its habitat use. This strictly nocturnal gecko, endemic to the western Mediterranean (Fig. 1), belongs to a monotypic genus of the Gondwanan family Sphaerodactylidae, mainly distributed in the Neotropics (Gamble et al. 2008), thus representing an outstanding biogeographical relict within the European fauna.

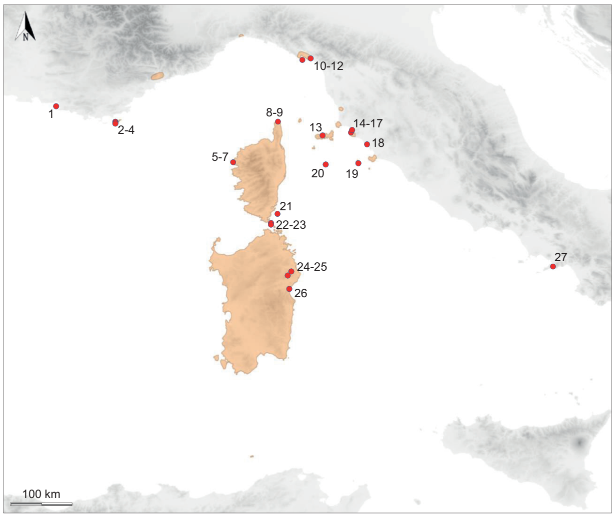

Figure 1. Distribution range the European leaf toed Gecko *Euleptes europaea* and geographic location of the observations of arboricolous behaviour reported in Table 1.

The European Leaf-toed Gecko is considered a rock-specialist and has several anatomical, behavioural, ecological adaptations to this habitat with which it is associated during its entire daily and life cycle (Salvidio et al. 2010). During the day, narrow rock crevices provide this species protection against predators and the opportunity to thermoregulate. Its small size, SVL 30–40 mm (Salvidio et al. 2010; Delaugerre and Corti 2020), its smooth (not keeled) body scales and its consequent ability to flatten itself to an extreme extent are probable morphological adaptations to crevice life. Crevices with openings as narrow as 3–5 mm permit this gecko to stay in both dorsal and ventral contact with the stone, preserving it from light and direct sun exposure and from desiccating cold winds, and providing optimal microclimatic conditions (thermal and hygrometric). Geckos are able to thermoregulate by conduction moving inside the shelter heated by the sun; whereas predators, such as birds, mammals, and other squamates, are too large to enter the crevices. In the roomiest cracks, large aggregations up to several dozen geckos may occur (Delaugerre 1981, 1992; Salvidio et al. 2010). Along with suitable climatic conditions, the availability and the quality of retreat sites and egg laying sites are likely the key factor governing the presence and the abundance of this gecko (Salvidio and Oneto 2008).

The nocturnal life of this species is also linked to the rocks. At night, *E. europaea* forages mostly on rocky surfaces (from horizontal to vertical to overhanging) that it climbs easily thanks to its distal toe pads and claws that allow attachment to dusty rock surfaces where other geckos with more powerful basal pads cannot do so -such as *Tarentola mauritanica*- (Russell and Delaugerre 2017). The heat stored by the rocks during the day is slowly released overnight making the rocks warmer than the air, wood, and other substrates, enabling this gecko to efficiently thermoregulate by thigmothermy during the night (Delaugerre 1984; Salvidio and Oneto 2008).

However, while the association of *E. europaea* to rocky habitats is well established, little is known about its ability to utilize vegetation near or far from rocks. For example, in the original description of this species it was reported that the species could be found under the bark of trees (Gené 1839), and recent observations suggest that, when rats are present, *E. europaea* shifts its spatial behaviour and feeds beneath vegetations (Delaugerre et al. 2019). Delaugerre (1992) also hypothesized that the animal may disperse in the vegetation during the hottest days of the year when the thermal supplement of the rocky substratum is no longer essential. Nevertheless, the arboreal aptitude of this gecko is still to be explored in order to have a more accurate view of its ecological niche and microhabitat use. Here we provided a comprehensive description of new field observations and a review of the available information on this topic that contribute to a refined view on the habitat use and arboreal abilities of *Euleptes europaea*.

Materials and methods

We collected observations of arboreal behaviour of *E. europaea* during field research in an opportunistic way. That is, vegetation was not primarily searched for the presence of the species but rather the species was accidentally spotted on vegetation while searching on rocks or for other species. Additional observations were gathered from colleagues and from the literature. We use the term "arboreal behaviour" in a broad meaning, including individuals climbing on trees, bushes, or low shrubs either dwelling on the bark, the branches or the leaves. For this tiny gecko, the main difference is likely dwelling on rock faces or on vegetation of any kind. On the other hand, we did not consider as 'arboreal behaviour' many observations we gathered during the years of *E. europaea* escape jumps (from heights of up to 3 m) toward other rock and into the vegetation, usually at the base of rock boulders, where they quickly disappear.

For each observation, we described the presence of the geckos on vegetation and their behaviour, and we reported the type of vegetation, the year and locality of the observations and the observers.

Results and discussion

A total of 32 observations of one or more individuals of *E. europaea* on vegetation were collected during 27 surveys. Observations cover 40 years (1982–2022) and 21 locations scattered across the species range (Fig. 1). Detailed information for each observation is reported in Table 1 and Suppl. material 2.

Eighteen different plant/tree species were used by *E. europaea*, mostly maquis species but also alien species such as *Eucalyptus* and *Asparagus aethiopicus* (Table 2). Although the opportunistic sampling does not allow proper statistical testing, the absence of large differences in observation frequency distribution across plant species (Table 2), suggests that the wide range of trees, bushes, and shrubs used by *E. europaea* reflects their availability at the sampling sites rather than plant selection by the gecko. Likewise, although our field research was mainly biased towards rocky environments (as this was considered as the elective habitat of *E. europaea*), and thus most observations concern vegetation growing on or nearby rocky surfaces, we also observed *E. europaea* on vegetation relatively far from rocks.

Arboreal behaviour of *E. europaea* was observed throughout the year, across the entire species range, on a wide variety of tree, shrub, bush species, on various parts of the plant (trunk, branches, fronds, twigs, leaves) at different heights above the ground (up to 3 m), strongly supporting that this is not an occasional behaviour of this species. This is further supported by a paper made available at the same time of our study that shows a high occupancy probability of *E. europaea* on *Eucalyptus* trees in an insular site (Deso et al. 2023). On the two *Eucalyptus* stands studied by these authors, *E. europaea* was the only gecko occupying the less-anthropized area. It is not yet known how high *Euleptes* geckos dwell in those trees and if this arboricolous habitat does provide egg-laying sites.

Table 1. Observations of arboricolous behaviour of *Euleptes europaea* (*Ee*); see Fig. 1 for the location of the observations. Island (I); islet (is).

Observation	Locality	Year	Period	Observer
1 *Ee* found on the nape of MD's neck while passing through bush by night	Scandula[5] (W Corsica)	1982	May	M. Delaugerre
Most of the *Ee* forage by night between the base of the granite and a mattress of plants	Lavezzu I[23] (S Corsica)	1986–2022	June to October	M. Delaugerre, C. Corti, M. Biaggini and P. Lo Cascio
2 *Ee* found on a bird nest box on *Arbutus unedo* (2 m high), not far from rocky boulders	Scandula (W Corsica)	1992	June	JL Martin
1 *Ee* in a bird nest box on *Erica arbora* (2 m high), not far from rocky boulders	Scandula (W Corsica)	1993	May	JL Martin
1 *Ee* climbing on *Rosmarinus officinalis* close to a schist face (Suppl. material 1: fig. S1a)	Port-Cros I[3] (Provence,	2003	October	M. Delaugerre
1 *Ee* climbing on *Lotus cytisoides* growing at the base of the rock (Suppl. material 1: fig. S1b)	Gabinière is[4] (Provence)	2003	October	M. Delaugerre
1 *Ee* climbing on *Malva arborea* (1.30 m high)	Toro is[21] (SE Corsica)	2005	April	M. Delaugerre
4 *Ee* (out of 23 diurnal sights) found under the bark of dead *Ulmus minor* trees	Tino is[10] (Liguria)	2006	20–29 June	F. Oneto, D. Ottonello, and S. Salvidio[a]
1 *Ee* found on the vest of MD while passing by bushes of *Juniperus phoenicea* (3 m high)	Rascas is[2] (Provence)	2008	17–18 June	M. Delaugerre
1 Ee found under the bark of *Eucalyptus* (Suppl. material 1: fig. S1c)	Giglio I[19] (Tuscany)	2008	August	S. Fattorini[b]
1 *Ee* climbing on *Anthyllis barba-jovis*, 3 m high	Cala Violina[14] (Tuscany)	2009	18 October	G. Radi
1 *Ee* head spotted among *Halimione portulacoides* (Suppl. material 1: fig. S1d)	Giraglia I[8] (N Corsica)	2012	6 October	M. Delaugerre
1 *Ee* found under the bark of *Juniperus phoenicea*; and 1 *Ee* found under the bark of *Cupressus* sp.	Cavallo I[22] (S. Corsica)	2014	6 November	V. Rivière
1 Ee found hidden under the bark of *Quercus ilex*	La Paolina is[11] (Tuscany)	2016	6 May	M. Delaugerre and C. Corti[c]
1 *Ee* on *Olea europaea* (1 m high)	Collelungo[18] (Tuscany)	2017	24 August	G. Radi
1 *Ee* foraging on the bark of *Juniperus Phoenicia* (1 m high)	Punta Ala[15] (Tuscany)	2019	30 September	G. Radi
1 *Ee* on *Anthyllis barba-jovis* (1.5 m high)	Punta Ala[16] (Tuscany)	2020	21 June	G. Radi
1 *Ee* on *Anthyllis barba-jovis* (2 m high)	Punta Ala[17] (Tuscany)	2020	5 October	G. Radi
>10 *Ee*, including a mating pair, observed by night on *Cistus* sp. and *Erica arborea* (2 m high; Fig. 2c)	Monte Albo[24] (Sardinia)	2021	6–7 July	E. Berrilli, M. Garzia, D. Salvi, and V. Gomez
>10 *Ee* observed by night on *Cistus* sp. and *Erica arborea* (1.5 m high; Fig. 2d)	Monte Albo[25] (Sardinia)	2021	8 July	D. Salvi, M. Garzia, and V. Gomez
2 *Ee* found under the bark of a fallen *Pinus halepensis* tree (geckos not active)	Positano[27] (Campania).	2022	5 February	F. Russo[d]
>20 *Ee* active by night on trunks of *Quercus ilex* and *Juniperus phoenicea*	Dorgali[26] (Sardinia)	2022	11–13 June	A. Macali and C. Pardo
1 *Ee* on a *Pinus halepensis* trunk, 2.5 m high	Montecristo I[20] (Tuscany)	2022	14 June	G. Radi and M. Zuffi
1 Ee found on the nape of MD's neck while passing through *Malva arborea* (1.5 m high) 1 *Ee* on the nape of MD's neck	Giraglia I[9] (N Corsica)	2022	2 August	M. Delaugerre
2 *Ee* sighted within *Opuntia ficus indica* pads	Pomègue I[1] (Provence)	2022	11 October	V. Lara and V. Rivière
1 *Ee* on *Asparagus aethiopicus* growing on a rock (Fig. 2e)	Tellaro[11] (Liguria)	2022	12 December	G. Bruni
10 *Ee* on *Pistacia lentiscus*, close to the rock face(Fig. 2a, b, f)	Tellaro[12] (Liguria)	2022	21 December	G. Bruni

1–27: sampling locality code as shown in Fig. 1.
[a]: reported in Oneto et al.(2008, 4)
[b]: reported in Corti et al. (2021, 54).
[c]: reported in Fattorini (2010, fig. 3).
[d]: reported in Di Nicola et al. (2022).

Table 2. Frequency of observations of *Euleptes europaea* on different plants and trees.

Species	N
Anthyllis barba-jovis	3
Arbutus unedo	2
Asparagus aethiopicus	1
Cistus sp.	2
Cupressus sp.	1
Erica arbora	4
Eucalyptus sp.	1
Halimione portulacoides	1
Juniperus phoenicea	4
Lotus cytisoides	2
Malva arborea	2
Olea europaea	1
Opuntia ficus indica	1
Pinus halepensis	2
Pistacia lentiscus	1
Quercus ilex	2
Rosmarinus officinalis	1
Ulmus minor	1

On vegetation this species rests, forages, and mates (Table 1). What is more important, *E. europaea* has been observed to move across branches and twigs with great agility, using its four members and its tail, and shows striking morphological adaptation to the arboreal lifestyle.

In low and thick vegetation, locomotion of *E. europaea* involves climbing, rather than crawling (on rock face), so that it may even "swim and vanish" in a puzzling way, in contrast to its relatively slow escape speed on rocks. In an arboreal context, it may perch head down as truly arboreal lizards do (Fig. 2a, c). Compared to rock faces, arboreal habitat is a much more structurally complex 3D array of branches and surfaces (Clark et al. 2021). This species' prehensile tail has long been recognized (Fitzinger 1843 p. 95; Wiedersheim 1876; Camerano 1885 p. 501; Mourgue 1910; Eijsden 1983; Bauer et al. 1997; Fig. 2c, d). Almost all adults bear a cartilaginous regenerated tail, turnip-like, enlarged for fat storage, that is still prehensile. The prehensile tail is a functional trait associated with the arboreal environment where this organ is used to grasp cork, branches, twigs and leaves (Mertens 1964; Eijsden 1983; Alibardi and Bonfitto 2019). The prehensile tail is also flexible and is an asset for equilibrium and the guiding of escape jumps (Jusufi et al. 2008; Fleming and Bateman 2012) and this species is a good jumper. Its tail is not only prehensile, it also bears terminal adhesive pads, even when regenerated (Eijsden 1983). In the arboreal context, tail pads supplement the muscular grapping of twigs or branches with dry adhesion of the sub caudal scansors (Fig. 2c, f and Suppl. material 1: fig. S1a, e). As stressed by Higham et al. (2017), in arboreal environments, when performing escape jumps or falls from trees, geckos land on leaves or smooth tree trunks. Arresting this fall requires a high loading of the adhesive system that is enhanced by an extra padded member, the tail. But these caudal adhesive systems are not the exclusive signature of arboreal lifestyle, since they are also used by geckos for climbing steep rock surfaces (Bauer 1998; Koppetsch et al. 2020) and to prevent the animal falling backward (Bauer and Russell 1994; Jusufi et al. 2008). Therefore, it is likely that these ecomorphological adaptations allow the European Leaf-toed gecko to exploit both rocky and arboreal microhabitats. To explain the origin of such ecomorphological adaptations to arboreal lifestyle we could speculate that these have been inherited by *E. europaea* from its European ancestors living in subtropical forests environments during Miocene (Estes 1969; Müller 2001; Müller and Mödden 2001; Böhme 2003; Čerňanský and Bauer 2010; Daza et al. 2014; Čerňanský et al. 2022).

Our study opens further questions also on the use of vegetated and wooded habitat by *E. europaea*. Could there be a continuum from i) a simple nightly coming and going from rocky habitat to nearby vegetation, as suggested by some observations, ii) to more seasonal wandering movements, ultimately turning back to rocky habitat for winter; iii) to truly arboreal living all year round? The rupicolous habitat niche of *E. europaea* is primarily driven by thermal constraints (Delaugerre 1984). These are particularly severe for a strictly nocturnal ectothermic vertebrate, inhabiting a temperate region where it colonizes Alpine elevations up to 1500 m (Delaugerre 1992). Rocky substrates typically have larger thermal inertia and a greater capacity for heat storage than soil or wood (Huey et al. 1989). Of course, this gecko is an active and efficient thermoregulator that uses the expansion and retraction of melanophores to speed up the acquisition of heat and to slow down its loss (Delaugerre 1984). But being a strict thigmotherm (it never basks) it would still need the rocky substratum for the primary acquisition of heat, during periods of thermal deficit, 5 to 6 months a year. Our finding of arboreal behaviour *E. europaea* in autumn and winter with air temperatures as low as 11 °C (Table 1) is therefore surprising. A possible explanation is that this species is able to locate warm environmental microclimates that retain higher temperatures throughout the night, allowing them to loosen the bond to rocks. The ability to exploit rare microclimates is especially important for nocturnal species, as heterogeneity of environmental temperatures is reduced at night compared to the day (Nordberg and Schwarzkopf 2019). However, understanding the apparent discrepancy between the thermal requirements of the species and its arboreal habits will require dedicated investigation.

In conclusion, to answer the main question of this study: is *E. europaea* a strictly rock-dwelling species? Definitely it is not. This species efficiently uses vegetated and wooded habitats, both in hot summer and colder winter nights, and shows adaptations to climbing and clinging for arboreal locomotion. It is a climbing gecko (opposed to ground dwelling), occupying both saxicolous and arboreal microhabitats like other geckos (Pianka and Pianka 1976; Norris et al. 2021).This realization has important implications for designing fieldwork research and management strategies for conservation. The evolutionary origin and ecological drivers for such behaviour remain to be fully investigated.

Figure 2. *Euleptes europaea* on *Pistacia lentiscus* **a, b, f** locality Tellaro, Liguria; photo by G. Bruni; on *Cistus* sp. **c, d** locality M. Albo, Sardinia; photo by D. Salvi; and on *Asparagus aethiopicus* **e** locality Tellaro, Liguria; photo by G. Bruni.

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Supplementary material 1

Euleptes europaea on various plant items

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Data type: figure (JPG image)

Explanation note: *Euleptes europaea* on *Rosmarinus officinalis* (**a**; locality Port-Cros island, Provence; photo by M. Delaugerre); on *Eucalyptus* (**b**; locality Giglio island, Tuscany; photo by S. Fattorini); on *Lotus cytisoides* (**c**; locality Gabinière islet, Provence; photo by M. Delaugerre); on *Halimione portulacoides* (**d**; locality Giraglia island, Corsica; photo by M. Delaugerre); on *Juniperus phoenicea* (**e**; locality Punta Ala, Tuscany; photo by G. Radi).

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Supplementary material 2

Observations of arboricolous behaviour of *Euleptes europaea*

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Data type: .docx / table

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