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Department of Biology

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Morphological and behavioral characteristics of sympatric populations of *Podarcis siculus* and *Podarcis melisellensis*

DOCTORAL THESIS

Supervisor: assoc. prof. dr. sc. Sofia Ana Blažević

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Morfološka i bihevioralna obilježja simpatričkih populacija *Podarcis siculus* i *Podarcis melisellensis*

DOKTORSKI RAD

Mentor: izv. prof. dr. sc. Sofia Ana Blažević

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Information about the mentor

Mentor: assoc. prof. dr. sc. Sofia Ana Blažević

Assoc. Prof. Dr. Sc. Sofia Ana Blažević, was born on May 30, 1983 in Buenos Aires, where she attended elementary school. At the age of 10, her family moved to Puerto Rico, where she continued her education through high school at Baldwin School of Puerto Rico. She began her university studies in Biology in 2001 at the University of Navarra, Pamplona, Spain. She moved to Croatia in 2003 and finished her studies in molecular biology at the University of Zagreb. She wrote her master thesis under the guidance of dr. sc. Sonja Levanat at the Laboratory for Hereditary Cancer, Department of Molecular Medicine, Ruđer Bošković Institute. In 2012, she received a Master's degree in Bioethics from the University of Navarra, Spain. In 2013, she received her PhD from the Department of Biology, Faculty of Science, University of Zagreb under the guidance of prof. dr. sc. Dubravka Hranilović with a dissertation entitled "Effect of perinatal administration of serotonin synthesis precursors or inhibitors of serotonin degradation on serotonin homeostasis in adult rats". Since January 2008, she has been employed at the Department of Animal Physiology, Department of Biology, Faculty of Science, University of Zagreb, first as a research assistant, then as a postdoctoral researcher and assistant professor, and from 2024 as an associate professor.

She explores monoamine systems and their role in shaping development, behaviour and physiology, combining neurochemical and behavioural approaches with analyses of genes involved in the monoamine and glucocorticoid systems to elucidate the influence of environmental factors, developmental stages, and ecological context on neurobiological function and stress responses. In her work, she uses comparative models – lizards of the genus *Podarcis* for neuroethological research, and rats and human populations for translational research. She collaborates with researchers in Croatia and abroad, including those at: the Faculty of Pharmacy and Biochemistry, the Faculty of Veterinary Medicine, the Institute of Anthropology, the Ruđer Bošković Institute, the Croatian Institute for Brain Research, the University of Buenos Aires and the Ludwig-Maximilian University in Munich. She has participated in several national and international projects (MSES, HrZZ, MZOŠ-DAAD). She lead a Croatian Science Foundation Installation Research Project "Dopamine Regulation of Competitive Behaviour of Lizards *Podarcis siculus* and *Podarcis melisellensis*" and the professional project "Implementation and Improvement of Professional Practice at the Faculty

of Science - ProSPer PMF", which led to the establishment of the Faculty of Science Career Center and the WorkIn' Science event. She established and continues to coordinate the LabAnim course for individuals working with laboratory animals.

She has co-authored 23 scientific papers in journals indexed in the Web of Science database and has presented her research findings at numerous international conferences. She has taught the courses Health Education and Chronicles of Scientific Research in Physiology at the undergraduate level, the courses Bioethics, Laboratory Animals in Science, Neuroimmunology, Applied Animal Physiology, Professional Practice and Laboratory Animals in Biological Research at the graduate level at the Department of Biology, Faculty of Science, University of Zagreb. She has served as supervisor of 8 master's theses, 22 graduate theses, and three doctoral dissertations. She is a member of the Croatian Society for Neuroscience (HDN), the Croatian Society for Laboratory Animal Science (CroLASA), the International Society of Education in Animal Sciences (ISEAS) and the Institutional Commission for Bioethics and Animal Welfare. She is fluent in Spanish, English, and Croatian.

University of ZagrebDoctoral thesis

Faculty of Science

Department of Biology

MORPHOLOGICAL AND BEHAVIORAL CHARACTERISTICS OF SYMPATRIC POPULATIONS OF *PODARCIS SICULUS* AND *PODARCIS MELISELLENSIS*

Tomislav Gojak, mag. biol. exp.

The widespread generalist *Podarcis siculus* is found in syntopy with the endemic *Podarcis melisellensis* along the eastern Adriatic coast. Behaviour, colouration and dorsal patterning of three syntopic populations from Croatia (Knin, Pag, Sinj) were examined to determine factors that could enable them to coexist. Antipredator responses were observed in the field, while activity, exploration, response to novelty and aggression were measured under laboratory conditions. Colouration was quantified as just-noticeable differences (JNDs) using bird and snake visual models. The strength of the dorsal pattern and how well it matches natural backgrounds was quantified using image analysis. The interspecific differences were in the timing and intensity of responses. *P. melisellensis* moved in shorter bouts, changed direction less frequently, approached novel objects later and rarely escalated contests with *P. siculus*. It also had a less conspicuous blue flank patch, fled shorter distances, and was better camouflaged against natural backgrounds, especially at Pag. Conversely, *P. siculus* contacted novel objects sooner, engaged earlier in more intense male contests, showed a more conspicuous flank patch, initiated escape sooner and fled farther. Behavioural response within individuals was consistent between repeated trials. These results suggest that exposure management is different between the two species, with *P. siculus* generally being more anticipatory in its approach to opportunities and its reaction to threats, while *P. melisellensis* responded later, only once an opportunity or a threat was close. Such an asymmetry could reduce direct interference at shared resources and allow for coexistence without strict spatial, trophic or temporal partitioning.

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MORFOLOŠKA I BIHEVIORALNA OBILJEŽJA SIMPATRIČKIH POPULACIJA *PODARCIS SICULUS* I *PODARCIS MELISELLENSIS*

Tomislav Gojak, mag. biol. exp.

Podarcis siculus, široko rasprostranjeni generalist, nalazi se u sintopiji s endemskom vrstom *Podarcis melisellensis* na istočnoj jadranskoj obali. Kako bi se utvrdili čimbenici koji omogućavaju njihov suživot uspoređeni su ponašanje, obojenje i leđni uzorak triju sintopijskih populacija u Hrvatskoj (Knin, Pag, Sinj). Antipredatorski odgovor procijenjen je terenskim opažanjima, dok su aktivnost, istraživačko ponašanje, odgovor na novitet i agresivnost mjereni u laboratorijskim uvjetima. Obojenje je kvantificirano kao jedva zamjetna razlika (eng. *just-noticeable differences*; JND) primjenom vizualnih modela ptica i zmija, a izraženost leđnog uzorka i njegova podudarnost s prirodnim pozadinama analizom slika. Međuvrsne razlike očitovale su se u vremenu i intenzitetu odgovora. *P. melisellensis* kretao se u kraćim naletima, rjeđe je mijenjao smjer, sporije je prilazio novim predmetima i rijetko je eskalirao sukobe s vrstom *P. siculus*. Imao je i manje uočljivu plavu bočnu pjegu, tolerirao je bliži prilazak prije bijega i pri bijegu prelazio kraći put, i imao je jaču podudarnost s prirodnim pozadinama, naročito na Pagu. Suprotno tome, *P. siculus* brže je dolazio u dodir s novim predmetima, ranije je ulazio u intenzivnije sukobe mužjaka, imao je uočljiviju bočnu pjegu te je ranije započinjao bijeg i pritom prelazio dulji put. Ovi rezultati upućuju na to da se dvije vrste razlikuju u upravljanju izloženošću: *P. siculus* u pravilu djeluje anticipacijski, i u pristupu prilikama i u reakciji na prijetnje, dok *P. melisellensis* reagira kasnije, tek kada su prilika ili prijetnja blizu. Takva bi asimetrija mogla smanjiti izravnu interferenciju na zajedničkim resursima i omogućiti suživot bez stroge prostorne, trofičke ili vremenske raspodjele.

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1. Introduction

1.1 Sympatry, competition, and the dynamics of coexistence

1.1.1 Sympatry

Species interactions are shaped by population distribution, commonly divided into the following types: sympatry, allopatry, parapatry and peripatry. Sympatry is when two or more closely related species coexist in the same geographic region and can interact [1, 2]. Allopatry is when geographic barriers keep ranges fully separate, parapatry when ranges connect with little overlap, and peripatry when a small population gets isolated at the edge of the main population's territory [3, 4, 5]. Species that live in sympatry are exposed to the same regional ecological conditions and form part of the same biotic community [2], though each species may use those conditions differently, even preferring different microhabitats within the shared range. Sympatric arrangements are prevalent across various taxa, including marine mammals such as dolphins [6], seals and whales [7], avians [8], reptiles [9], insects [10], plants [11], fungi [12], and microbes [13]. When species that are morphologically similar or phylogenetically close share the same habitat, they are usually dependent on the same limited resources [14, 15].

Gause's Competitive Exclusion Principle states that "complete competitors cannot coexist", meaning that two species competing for the same limited resources cannot persist together over prolonged periods [16]. The species that has even a slight competitive advantage should, over time, take over and force out its closest competitor [16, 17]. Gause examined this hypothesis through laboratory experiments with *Paramecium* species [17], while Park observed comparable trends in *Tribolium* flour beetles [18]. In both cases, in controlled environments, one species consistently removed the other [17, 18]. However, natural communities often have multiple species that live alongside one another and exploit the same resources. This discrepancy between theoretical prediction and empirical observation — termed by Hutchinson the "paradox of the plankton" [19] — has sparked decades of research in community ecology [20]. Explaining how competing species nonetheless persist together is central to understanding community assembly and the outcome of biological invasions.

Within a region, two sympatric species do not necessarily occupy the same habitat. Rivas (1964) introduced the term syntopy to describe the case in which species share both the region and the local habitat at the same time [21]. Syntopy is the spatial scale at which competitive exclusion is most likely to operate, because resource overlap is direct rather than potential.

Understanding how sympatric species share resources explains how communities form [22], how ecosystems remain stable [23], and how ecosystem functions, such as nutrient cycling and primary productivity, are maintained [24]. As climate changes, habitats fragment, pollution spreads [25], and invasive species occupy novel habitats [26], more species are brought into sympatry, and how they coexist becomes a question for environmental management.

1.1.2 Interspecific competition

Interspecific competition is a mutually detrimental interaction (-/-) among individuals of different species that compete for one or more limited resources [14]. The existence of one species diminishes resource availability for the other, hence decreasing fitness - assessed through survival, growth, or reproductive success - in both populations [27]. If there were no limits on resources, populations would grow without limit, and competition would be reduced to a minimum [14]. In nature, resources are always limited. This is why field experiments detect competitive effects in most systems examined, although the strength of these effects varies widely among taxa and resources [27].

The specific resources in question depend on the species and their ecological needs. Food is often a limiting resource and a major source of competition in animal communities [28]. For instance, various raptor species hunt the same rodents [29], several dolphin species exploit common fish and cephalopod species [30], and numerous terrestrial animals, including many lizards, consume the same insect species [31, 32]. Furthermore, direct competition is observed between spectacled cobras (*Naja naja*) and oriental ratsnakes, which both hunt the same populations of snakes, mammals, and frogs [33].

Another common point of conflict is space, which includes areas defended for foraging or mating [34], nesting or denning sites. Competition for preferred microhabitats can be determined by vegetation structure or abiotic factors (perch locations used by different *Anolis* species are a classic example) [35]. Interspecific competition often occurs via two separate

mechanisms: indirectly through exploitation and directly through interference. Exploitation is when species impact each other exclusively by exhausting common resources [14, 28]. Even if individuals never encounter one another, one species can take up more resources, leaving less for the other. Exploitative competition need not involve any direct contest. Simply being first to reach a food item, basking surface, or refuge can be enough to deny it to a competitor, so differences in how quickly individuals locate and reach resources can translate directly into differences in access [10]. Success usually depends on how quickly or efficiently resources can be collected [36]. Examples include plants that capture light or soil nutrients before their neighbours [37], and faster foragers or smaller individuals whose intake rates are high relative to their demands [38].

Interference is when individuals of different species aggressively restrict each other's access to resources [14, 28]. This includes overt hostility, fights, territorial responses, kleptoparasitism, and the synthesis of allelopathic compounds in flora and microorganisms. Dominant animals may physically prevent subordinates from accessing territories or food locations [39]. For example, ants may obstruct the entrances of competing colonies' nests [40]. Interference typically advantages larger or behaviourally dominant individuals. However, the benefit of resource monopolisation has direct costs in energy, time, survival, and lifetime reproductive output [27]. Exploitation and interference are not mutually exclusive; numerous competitive interactions incorporate aspects of both [14].

Beyond exploitation and interference, interspecific competition can also operate indirectly through apparent competition, when species have shared natural enemies. In apparent competition, two species that do not compete for the same resources negatively affect each other by sharing a common predator, parasite, or pathogen [41]. An increase in the abundance of one species boosts the population of the shared enemy, which in turn increases mortality on the other species. Apparent competition can exert a stronger influence on community structure than direct resource competition [41, 42] and becomes especially relevant where predation pressure is intense.

Competition between species is frequently uneven: one species bears a disproportionately larger fitness cost than the other [28]. Such asymmetric competition is widespread among closely related species that differ in body size or behavioural dominance [43], and its effects range from niche displacement of the weaker competitor to driving it locally extinct. This

strong asymmetric interference competition has repeatedly been the case for the larger and behaviourally dominant *Podarcis siculus* (Rafinesque-Schmaltz, 1810) that has been shown to competitively displace other species of its genus such as *Podarcis melisellensis* (Braun, 1877) [9].

The Lotka–Volterra competition equations offer a formal way to capture these dynamics [44, 45]. Stable coexistence requires each species to limit its own growth more strongly than it limits the growth of the other [46]. Because this framework assumes constant conditions, it cannot capture the environmental variability and chance events that also shape competitive outcomes in nature [46, 47]. Such variability can relax the limits on how similar coexisting species may be, allowing them to coexist in cases where the simpler prediction would predict exclusion [48].

The ecological effects of interspecific competition are damaging to the species in question. Fitness decreases: survival begins to decline, growth stagnates, and reproduction decreases [27]. A species may be limited to a stricter range of resources or habitats than its fundamental niche (the niche it would inhabit in the absence of competition) permits, and its realised niche decreases [49]. Ecological release, a process in which a competitor is removed, and the niche breadth increases, shows that this kind of compression occurs [10]. Competition can also force weaker species into suboptimal environments [49, 50], and in the worst circumstances, it can completely remove them from a shared habitat [17]. Despite these competitive pressures (and the additional influence of dispersal, genetic drift, and environmental fluctuation), coexistence is common. The primary mechanism of coexistence is niche partitioning: coexisting species use shared limiting resources differently, by diet, space or time, and so stay below the limiting-similarity threshold that constrains how similar competitors can be [10, 35, 51, 52].

Competition may trigger the development of evolutionary changes. Character displacement happens when traits vital for resource acquirement differ more in sympatric populations than in allopatric ones [53, 54], making the niches less similar. This phenomenon is well illustrated in *Anolis* lizards on Caribbean islands [35]. These lizards have gone through adaptive radiation, which has led to the formation of various “ecomorphs”. These are species groups that share a general body form but differ in fine-scale traits and behaviours adapted to specific forest microhabitats. By dividing up spatial niches that range in desired perch height and

diameter, several *Anolis* species can live in the same forest without direct competition. Competition functions as a selection pressure, connecting ecological interactions to evolutionary pathways and influencing species' roles and ranges [35, 53].

1.1.3 Intraspecific competition

Understanding interspecific competition alone is insufficient for predicting competitive outcomes; coexistence also depends on how strongly populations regulate their own size and composition [46]. Competition for limited shared resources among conspecific individuals can equal or exceed the effects of interspecific competition on population and community dynamics [46]. Since conspecifics possess essentially identical ecological requirements, the probability of resource overlap and conflict is therefore increased [14]. Because each additional conspecific individual draws on the same resource base, intraspecific competition is inherently density-dependent: its intensity increases as population density rises, generating the negative feedback that constrains population growth [55, 56, 57]. The same feedback operates in mobile animals: experimentally lowering neighbour density raised reproduction in a territorial songbird [58] and, in a tree lizard, individuals down-regulated contest performance at high density, easing aggressive conflict [59].

When more individuals concentrate in the same area, each has less food, water, space, and access to mates, and fitness decreases accordingly [56, 60]. Where each population suppresses its own growth more than it suppresses that of its competitor [46], no single species monopolises the shared resource, and rarer competitors retain enough access to food, space, or mates to sustain their populations. Most direct tests of this self-limitation come from plants [61] and plankton [62], but it has now been measured in animals as well: in *Enallagma* damselflies [63], *Anolis* lizards [64], and coral-dwelling fishes [65]. That animal evidence is still scarce and inconsistent, since in some of these systems intraspecific and interspecific competition proved comparable rather than consistently stronger within species [63, 66].

Intraspecific competition follows the same exploitation and interference routes as interspecific competition [14], but increased conspecific population causes additional feedback loops beyond simple resource depletion. One well-documented mechanism is physiological stress from frequent social interactions, which is reflected in higher glucocorticoid levels [67]. This stress can cause behavioural alterations, such as increased aggression [67], a shift in the trade-

off between foraging and vigilance [68], increased dispersal (the movement of individuals from natal to breeding sites or between breeding sites [69]) rates [70], and shifts in parental care strategies that may reduce offspring investment [71]. Large populations also have a higher risk of disease and parasite transmission as individuals interact with one another more frequently, and persistent stress weakens the immune system [72]. High density can also increase the danger of predation, because predator numbers and per-capita kill rates both track prey density; in moose (*Alces alces*), predation rate is density dependent up to about 0.65 animals per km² and inversely density dependent above it [73]. These physiological and behavioural responses together demonstrate that density dependence operates via several, interconnected channels rather than a single system [74]. These channels are not alternatives to exploitation and interference: stress, disease and predation risk fall on the same individuals that are already competing, so their effects add to it [75].

1.1.4 Aggression and agonistic behaviour

Interference, as described above, is expressed most directly as agonistic confrontation rather than as the diffuse depletion of shared resources that characterises exploitation. Examining the strategies, causes, and processes of these encounters is critical to understanding what happens when two sympatric congeners encounter one another. Agonistic behaviour includes the whole conflict cycle, which includes initial attack, threat display, defensive response, submission, pursuit, and withdrawal [76]. Overt aggression is the most noticeable feature, although it is merely one component of a larger repertory [77].

Every agonistic interaction includes a cost-benefit analysis [78]. On the benefit side, there are fitness-related resources like mates, food, and territory [79, 80]. The costs include energy spent fighting, physical injury or death, increased predation vulnerability during the combat, stress hormone surges, and the opportunity cost of time not spent on other activities [78]. Direct physical fights are rare: most aggressive interactions are settled through display, with opponents assessing each other's fighting ability before escalating [81]. Evolutionary game theory formalises this. The Hawk-Dove game [82], building on Maynard Smith and Price's analysis of animal conflict [83], explains the rarity of escalation and the prevalence of ritualised assessment displays, particularly where the cost of injury exceeds the value of the contested resource.

When individuals aggressively interact with each other frequently, they tend to develop dominance hierarchies, and once the ranks are set these hierarchies make it less expensive to keep fighting [79]. A single contest can have long-lasting effects on both the winner and the loser. Among these effects, modifications in an individual's hormonal balance and self-evaluation influence its performance in subsequent interactions [84]. The expressions of agonistic behaviour and the results of competitions possess distinct physiological foundations. Androgens, particularly testosterone, exhibit a robust and consistently reproduced association with aggression [85]. This connection frequently operates in both directions, as participation in a competition can alter hormonal patterns [85].

Agonistic encounters are physically demanding, so energy reserves and body condition matter [78]. Individuals in better energetic and physiological condition have a greater tendency to fight for an extended period or with a lot of force [78]. Seasonal cycles, often associated with reproduction and concurrent hormonal fluctuations, significantly influence animal aggression [85, 86]. Habitat structure — which affects visibility, refuge availability, and territorial defensibility — also shapes the dynamics of agonistic interactions [87].

1.1.5 Coexistence

Stable coexistence is favoured when each species is more strongly limited by competition with conspecifics than by competition with heterospecifics [46]. When a species becomes rare, intraspecific competition weakens, allowing its population to recover and thereby reducing the likelihood of competitive exclusion [90]. This self-limitation mechanism also extends to multispecies communities [89].

The incorporation of temporal dynamics (e.g. the storage effect) and cross-trophic interactions (e.g. predator-mediated coexistence) has transformed coexistence theory. While classical models based on competitive exclusion and niche partitioning established its conceptual foundation, they failed to explain the persistence of high species diversity in communities with substantial resource overlap [19, 94]. Contemporary theory addresses this gap by recognising that environmental variability and top-down regulation modify competitive outcomes, allowing coexistence to emerge under both stable and fluctuating conditions.

Contemporary coexistence theory identifies several processes that maintain this equilibrium and preserve species variety: niche differentiation, the storage effect, predator-mediated

coexistence, and spatial environmental heterogeneity. Niche differentiation makes individuals compete more strongly with conspecifics than with heterospecifics. It ultimately reflects the balance between niche differences that stabilise coexistence and average fitness differences between competitors [46, 90].

The storage effect is a fluctuation-dependent coexistence mechanism whereby species accumulate the benefits of favourable periods in long-lived life stages (e.g. dormant eggs, extended lifespans) and draw on them during unfavourable ones, allowing rarer species to recover [91]. The storage effect requires: (1) temporal environmental variability, (2) species-specific reactions to this variability, (3) the tendency for competition to escalate under favourable conditions (covariance between environment and competition), and (4) a mechanism to mitigate population growth, such as dormant seeds or eggs or extended lifespans [91]. In effect, species partition the changing environment over time.

Predator-mediated coexistence operates when natural enemies such as predators, parasites, and viruses have an unequally detrimental influence on the most common or dominant species [92, 93]. This approach necessitates that natural enemies exhibit density-dependent effects on the dominant competitor or alter their tendency to focus on the most abundant prey species [41, 92]. By keeping the better competitor from getting to population numbers that are high enough to keep other species out, such mortality levels the playing field and helps keep diversity.

Changes in the environment (e.g. type of soil, the temperature, and the amount of precipitation) or the amount of resources in each location can create patches where different species have competitive advantages [36]. This mechanism is based on local variation of parameters influencing competitive capability and dispersal between patches. In its preferred patches, intraspecific competition outweighs interspecific competition. The physical structure of the environment can stabilise competitive networks, which can lead to spatial niche partitioning and allow for regional coexistence through dispersal.

In fact, coexistence is better thought of as an ongoing non-equilibrium process rather than a fixed stable state [94, 95, 96]. Ecological interactions and the evolutionary responses they provoke continually reshape patterns of competitive dominance and subordination [97, 98]. Environmental change, species introductions, and local extinctions can all upset the

competitive balance [25], and because competition keeps favouring traits that improve resource acquisition and competitive performance [53], these species effectively function as moving evolutionary targets.

This contemporary perspective is directly related to the Eastern Adriatic *Podarcis* system. *Podarcis* (Lacertidae) is a diverse group of small lacertid lizards that evolved in the Mediterranean basin between the late Miocene and Pliocene [99]. Several species, including *P. melisellensis*, *P. siculus*, and *Podarcis muralis*, overlap broadly across the Eastern Adriatic coast and its islands, where they are often found in sympatry [100, 101]. There, *P. siculus* has repeatedly displaced *P. melisellensis* from preferred habitats [9, 102, 103]. However, absolute exclusion is not universal. The two species coexist in significant portions of their shared range [101, 104]. This calls for a deeper look into the factors that inhibit competitive exclusion in locations where it may typically be predicted.

1.2 Study system

1.2.1 Genus *Podarcis* as a model

Podarcis is a lizard genus belonging to the family Lacertidae; it includes around 25 species spread throughout Europe's reptile fauna [100, 105]. They are small, diurnally active, and primarily insectivorous [100, 104]. Several of the species are endemic to Mediterranean islands. Owing to their biodiversity and presence across diverse terrestrial and insular ecosystems, *Podarcis* lizards provide suitable models for both ecological and evolutionary studies. They may be one of the most suitable genera to examine rapid evolutionary change due to the fact that island populations have shown remarkable examples of morphological and ecological changes occurring over relatively short time scales [106], which likely include behaviour. Two species, *P. siculus* (Italian Wall Lizard) and *P. melisellensis* (Dalmatian Wall Lizard), are commonly sympatric across the Adriatic, and their interactions which are often mediated by behavioural mechanisms, are central to the questions of coexistence versus competitive displacement in the region [107, 108, 109, 110].

1.2.2 *Podarcis siculus* (Italian Wall Lizard)

P. siculus is a medium-sized diurnal lacertid native to the Italian Peninsula, Sicily, the northern Adriatic coast, and several Mediterranean islands including Corsica [104, 111, 112].

Adult snout-vent length typically ranges from 60 to 90 mm [112]. The dorsal colouration is typically green to olive-green with darker reticulation along the flanks; ventral colouration is whitish to pale yellow, with two ventrolateral blue patches present in both sexes but typically larger and more chromatically distinct in adult males. Sexual dimorphism is evident in both study species, and in *P. siculus* males are substantially larger [104]. Larger body size and its performance correlates, such as bite force, influence contest-relevant capacities in *Podarcis* [113], and dominance disputes among males are the likeliest context for this advantage.

Ecologically, *P. siculus* is a generalist with high tolerance for anthropogenic landscapes, occupying habitats from unaltered forest and coastal scrub to drystone walls, urban edges, agricultural margins, and other human-created structures [104, 114]. While primarily insectivorous, it shows clear dietary flexibility, supplementing invertebrate prey with plant material in some populations [106]. This ecological breadth accompanies an expansion well beyond the native range, with introduced populations established across the Mediterranean, elsewhere in Europe including the Iberian Peninsula, the United Kingdom, and the Netherlands, in Turkey, North Africa, and North America [103, 114, 115, 116]. It is plausible to associate this colonisation success with behavioural traits (including increased exploration and decreased risk-aversion of novel stimuli) that could contribute to successful establishment in novel habitats [102, 117, 118]. The combination of ecological generalism with a rapid ability to adapt locally to new conditions likely contributes to both the extent of the native range and the invasive capabilities of the species [102, 106, 109, 117]. Adriatic populations show high baseline activity, frequent novelty engagement, and consistent individual differences in exploratory and aggressive behaviour [119], and populations across the non-native U.S. range likewise show consistent behavioural variation in bite force and exploration [120].

1.2.3 *Podarcis melisellensis* (Dalmatian Wall Lizard)

Podarcis melisellensis, the Dalmatian Wall Lizard, is a small to medium-sized lacertid endemic to the eastern Adriatic coastal zone and its surrounding islands [100, 101]. Populations occur along the Croatian coast and offshore islands, in the coastal zone of Bosnia and Herzegovina, in Montenegro, and locally in northern Albania [121]. Despite this restricted range, the species is currently assessed as Least Concern on the IUCN Red List [122]. Within the European Union, it is listed in Annex IV of the Habitats Directive (92/43/EEC) among

animal species of Community interest in need of strict protection [123]. Adult snout-vent length ranges from approximately 50 to 75 mm, with males averaging slightly larger than females [113]. The dorsal colouration is typically brown to grey-brown with darker dorsolateral and lateral stripes; ventral colouration is white to pale yellow. Blue ventrolateral patches are present in both sexes but are smaller and less chromatically distinct than in several congeneric *Podarcis*. Reference genomes have recently been published for both study species [124, 125]. Ecologically, *P. melisellensis* is closely associated with karst and rocky habitats. Typical localities include drystone walls, limestone outcrops, rocky pasture margins, and sparse Mediterranean shrubland, and the species is most abundant in structurally complex rocky habitats with frequent refuge openings [104]. The diet is primarily insectivorous, dominated by ants, beetles, spiders, and small dipterans; plant material is rare in stomach-content analyses [126]. Interspecific interference can affect thermoregulation in lacertids including *P. melisellensis* [127], and morphological variation among Croatian populations is reflected in whole-animal performance (sprint speed, bite force) relevant to refuge use and escape [113].

Colour polymorphism exists in some populations of *P. melisellensis* (white, yellow or orange ventral colouration). Each colour morph is associated with variation in body size, head morphology, biting force capacity and microhabitat selection [128, 129]. Such colouration may serve as camouflage, play a role in mate selection or signal dominance.

1.2.4 *Podarcis siculus* and *P. melisellensis* interspecific dynamics

Due to *P. melisellensis* status as an Adriatic endemic [121], its interaction with the invasive *P. siculus* is a conservation concern. When sympatric with *P. siculus*, *P. melisellensis* often prefers microhabitats, especially stonewalls [101]. This preference for structural refuges may reflect the species' anti-predator strategy. Alternatively, if encounters with the larger and more aggressive *P. siculus* raise the perceived risk of unfamiliar situations, *P. melisellensis* may express stronger neophobia where the two species co-occur. It is therefore expected to be at a disadvantage in encounters dominated by aggression rather than habitat-specific performance [9, 117].

The Adriatic archipelago is a natural laboratory for studying interspecific dynamics between *P. siculus* and *P. melisellensis*. A primary driver of the interaction between the two species is

likely to be direct behavioural interference, with *P. siculus* behaviourally dominant [9]. While the neurochemical basis for these differences has been suggested to relate to differing levels of certain monoamines in the brains of the two species [130], the causal relationship has yet to be demonstrated. There is evidence that *P. siculus* exhibits more extensive exploratory behaviour than *P. melisellensis* in some contexts [117], which would give the former a potential additional competitive advantage. The two species also differ in colouration, and each also varies within species: *P. melisellensis* displays ventral colour morphs [128], while *P. siculus* shows dorsal-pattern polymorphism among populations [131]. This variation may also play a role in predator avoidance and social signalling that affects how the two species interact.

Competitive exclusion of *P. melisellensis* by *P. siculus* has been demonstrated at multiple Adriatic locations [9, 115, 117], and the most dramatic example is documented on Pod Mrčaru Island. *P. siculus* was introduced to Pod Mrčaru Island in 1971 and quickly underwent significant, well-documented changes in its morphology [106]. The original *P. melisellensis* population on Pod Mrčaru Island has been replaced by *P. siculus* [106, 109], and recent genomic analyses found no evidence of admixture between the two species, indicating replacement without hybridisation [132]. The Pod Mrčaru system illustrates the capacity of *P. siculus* for rapid phenotypic change (e.g., development of cecal valves associated with increased herbivory) in response to environmental pressures [106].

1.3 Behavioural traits in sympatric coexistence

1.3.1 Behavioural traits and consistent individual variation

Behavioural variation among individuals and species is commonly organised into a small number of repeatable axes. Following the framework of Réale et al. [133], the relevant traits are exploration, activity (together described as movement), the two responses to novelty (neophilia and neophobia), boldness, and aggression; the sections below define each and explain how differences in them can reduce competition and support coexistence.

Exploration is an individual's drive to seek and gather information about novel settings or stimuli; it is conceptually distinct from boldness, which concerns the response to danger rather than to novelty [133]. Within Réale et al.'s framework, exploration is captured by latency to approach, contact frequency with novel cues, and the rate at which an individual

samples an unfamiliar environment [133]. What a high exploration score actually reveals varies between studies: in some it captures fast-paced scanning of the environment with considerable locomotion, while in others it reflects a slower but persistent movement through unfamiliar surroundings over a longer period [134]. In lizards, the fast-scanning form is well documented, since invasive *P. siculus*, for example, is quicker than its congeners to investigate novel stimuli [117], whereas the slower, persistent form has been described mainly in birds [134].

Activity, by contrast, is not an exploratory trait; it refers to an individual's overall level of movement, typically measured as the proportion of time spent in active locomotion within a standardised arena or observation period, and is therefore assessed in a familiar context that captures baseline movement tempo rather than a response to novelty [133]. In many lizards, locomotion is not continuous but alternates between bursts and pauses, a pattern formalised as intermittent locomotion [135]. Within lacertids, such burst-and-pause movement in open space has been documented in *Lacerta vivipara* [136], and foraging-mode studies distinguish sustained search from more discontinuous movement [137, 138]. The proportion of time spent moving versus paused, and the angular velocity during movement, are therefore not redundant measures of activity. Activity correlates with thermal microhabitat use and foraging strategy and is a stable, between-species behavioural trait in lacertid lizards [119].

Novelty modulates an individual's exploratory behaviour, expressed through two distinct responses: neophobia (avoidance of, or hesitancy towards, novelty) and neophilia (attraction to, or interaction with, novelty) [139]. Differences in these traits between species can drive divergence in diet breadth and use of novel microhabitats, influencing niche partitioning [140]. Neophilia and neophobia are best understood as distinct dimensions rather than opposite ends of a single axis, potentially mediated by separate mechanisms [141]. Neophobia, which involves the cognitive classification of a stimulus as novel on the basis of prior experience, is thereby distinguished from general fearfulness or boldness [142]. Functionally, while high neophobia can constrain resource discovery through risk avoidance [143], neophilia promotes investigation, learning and innovation [144]; indeed, reduced neophobia is frequently linked to success in human-modified environments [145]. Because these reactions are highly context-dependent (influenced by internal state, experience and setting [146]), experimentally isolating responses specifically to novelty requires careful

methodological design, often presenting novel stimuli within familiar environments [142, 146].

Boldness (or shyness) reflects an individual's general willingness to take risks in unexpected or hazardous situations [133]: bold individuals investigate unfamiliar objects and enter open areas that shy individuals avoid [147]. It is therefore related to, but distinct from, the response to novelty: it concerns danger rather than novelty as such, even though the two often covary [133]. In practice it is assessed from responses to risk, such as how quickly an animal retreats to shelter after a disturbance [133, 148]. Differences in risk-tolerance can in turn let sympatric species partition a risk gradient, with bolder individuals exploiting more exposed but richer microhabitats [149, 150].

Aggression is the readiness to launch attacks or direct threats at other individuals [147]. It is especially prevalent where food, territories or mates are limited, and it underlies the formation and maintenance of dominance hierarchies. In many lizard species these aggressive interactions are male-biased, so dominance signalling and contest outcomes can differ between the sexes [151, 152]. Aggression is most often measured by the latency to initiate aggressive acts, the frequency and intensity of displays, chases, lunges and bites, and the spatial distance maintained between interacting individuals [152].

Individuals frequently exhibit consistent changes in behaviour across time or contexts [153]; they are not uniform automatons performing species-specific behaviours. It is now understood that such variation is structured, repeatable across time and context, and shaped by natural selection [133]. Because behaviour is the major channel through which organisms interact with their surroundings (acquiring food, dodging predators, finding mates, competing with rivals [154]), the specific behavioural profile an individual exhibit in competitive settings has significant ramifications for its fitness [27].

Repeatability, the proportion of behavioural variation that lies between rather than within individuals, quantifies the consistency required for individual-level behaviour to have ecological consequences [133, 155]. Statistically, a trait is repeatable when variation between individuals exceeds variation within individuals across repeated observations, although even highly repeatable behaviours retain some within-individual variation [133]. Consistent inter-individual differences in aggressiveness, for example, can influence the outcome of contests

[133]. These traits are difficult to define and measure because definitions overlap and different assays capture different facets of behaviour, so careful operational definitions and methodological validation are essential [133, 156]. Such consistency carries ecological costs as well as benefits: a bold or aggressive individual tends to behave the same way across contexts, even when this is disadvantageous [147]. This carry-over, sometimes called behavioural spillover, means that a tendency useful in one setting can become harmful in another. A lizard whose high activity aids foraging, for instance, may stay equally active when a predator appears, raising its predation risk [147].

Trade-offs of this kind are the norm rather than the exception [157]. Understanding these trade-offs matters for explaining why multiple behavioural strategies persist within populations instead of a single strategy reaching fixation [147]. Part of the answer lies in environmental heterogeneity, spatial and temporal fluctuation in predation pressure, resource abundance, and social context means that no single strategy consistently delivers the highest fitness [147, 158, 159]. Under those conditions, selection cannot eliminate alternative behavioural types, so variation is maintained [147]. Maintaining this variation is central to understanding how species like *P. siculus* and *P. melisellensis* develop distinct behavioural profiles that shape their ecological dynamics. Stable individual differences of this sort shape species interactions, dispersal patterns, niche specialisation, and both the direction and pace of evolutionary change [147, 157].

1.3.2 Behavioural plasticity as a competitive strategy

Although consistent behavioural tendencies point to underlying predispositions, animals are not locked into fixed responses: they can adjust what they do when circumstances shift, a capacity referred to as behavioural plasticity [160]. When such adjustment concerns the timing and context of an existing behaviour rather than its form, it is termed behavioural flexibility [161, 162]. This flexibility lets individuals tune their actions to local conditions, helping them deal with competitive pressure and cope with environmental unpredictability across their lifetimes [163]. Behavioural plasticity is the capacity of an individual to alter its behaviour in response to changing environmental or social conditions [160]. Two broad categories of behavioural plasticity are usually recognised [160]: developmental plasticity, in which environmental experience during ontogeny shapes the adult behavioural phenotype, and activational plasticity, in which an individual reversibly modifies its behaviour in

response to current conditions. This second form allows animals to fine-tune their behaviour on shorter timescales, for example adjusting foraging effort in response to perceived predation risk or modulating aggression when competitors are nearby [84].

Competitive encounters are among the most potent drivers of plastic behavioural responses. Animals routinely adjust their strategies according to competitor density, the identity of a rival, the value of the contested resource, and their own prior experiences. Population density strongly affects how often and how intensely competitive interactions occur, and typically elicits plastic shifts in aggression [77]. As density rises, encounters become more frequent and hostility generally increases because resources grow scarcer [164]. The relationship is not always straightforward, however; aggression can peak at intermediate densities, since sustained fighting at very high densities may simply cost too much [77]. The social makeup of a group within a given density also matters. Work on *Drosophila melanogaster* has shown how strongly aggression depends on the social composition of the group. Males adjusted their aggressiveness to the genotypes present around them, fighting more in groups that contained a more aggressive third male, with measurable consequences for mating success [165].

Animals also change their behaviour in response to competitor identity [166]. Interactions with conspecifics and heterospecifics can elicit distinct responses. *P. siculus* is an excellent example of this point. Along the Adriatic coast, the species appears to replace *P. melisellensis* through direct interference, i.e. aggression [9]. However, in Lisbon, where *P. siculus* coexists with the native *Podarcis virescens*, the competitive mechanism appears to be completely different: *P. siculus* obtains an advantage by arriving at food patches first and consuming more effectively, with minimal overt aggressiveness toward *P. virescens* (as explained in [102]). The ability of one species to switch between interference and exploitation competition depending on the opponent suggests remarkable plasticity, which is likely to drive some of its invasive success.

Even within a species, the level of aggression varies. Weaker aggressive responses are evoked by familiar neighbours — the “dear enemy” effect [167] — while aggression consistently increases when a contested resource is regarded as more valuable [167, 168]. Responses to novelty are equally variable: predator neophobia toward unfamiliar prey shows wide variation across taxa and contexts [169], social learning can diminish neophobia (observing a conspecific safely handle a new object reduces avoidance [170]). Perception of fearful stimuli

triggers measurable endocrine and physiological responses that in turn promote avoidance, flight, or withdrawal behaviours [142].

More broadly, behavioural plasticity is seen as adaptive because it allows organisms to fine-tune their phenotype to current conditions without having to wait for genetic change over generations [163]. Its rapid plasticity can protect entire populations from habitat alteration or anthropogenic disturbance, acting as a temporal bridge until slower evolutionary processes catch up [163]. The success of many invasive species and adaptation to urban environments is frequently attributed, at least in part, to high behavioural plasticity [171, 172, 173].

Behavioural plasticity has limitations. Consistent behavioural features limit how far and in what direction an individual can modify its behaviour [147], while adaptive plastic responses rely on environmental cues that are actually present and give reliable information [174, 175]. When cues are vague, unexpected, or simply lacking (for example, when a cue that formerly predicted risk or reward no longer does so in a changed environment), the induced response can be mistimed or misdirected, and therefore maladaptive [174]. There are additional maintenance costs: the increased neural investment required for flexible behaviour is both energetically and developmentally expensive [160]. Even species with high behavioural flexibility may find its speed or scope insufficient when confronted with quick or severe environmental change [176].

1.3.3 Behavioural adaptations and coexistence in sympatry

Closely related species that are also morphologically similar face a clear challenge when they occupy the same location: their resource needs overlap heavily, and competition follows [177, 178]. Phenotypic differences, whether genetically fixed or plastically developed, offer a route around this challenge by reducing niche overlap sufficiently to permit coexistence [177]. Such niche partitioning lets several ecological strategies coexist [10], and behavioural distinctions, rather than morphological or physiological ones, frequently keep competitive interactions from resulting in competitive exclusion [46].

Where sympatric species differ along these behavioural traits — in exploration tendency [133], attraction to novelty [139], general activity [179], boldness, and foraging technique [180, 181] — those differences can reduce direct competition. They are not, however, without cost: higher exploration exposes individuals to greater predation risk [182], and sustained high

activity is energetically expensive [180]. Variation in exploration intensity, from active search to sit-and-wait, further determines how broadly individuals encounter and exploit resources within their range [180, 183]. Differences in exploratory and activity profiles often reflect contrasting energy-management strategies, from low-activity, energy-conserving patterns to high-activity, energy-intensive ones [180, 183], and these shape feeding strategy, habitat selection and dispersal [139, 180, 181, 183].

The criteria used to evaluate exploration — total distance moved, number of discrete movement intervals, and cumulative time spent moving — are ultimately proxies for both search effort and the energy an animal invests in the process [184]. Angular velocity (turning rate) adds a further dimension: animals that turn frequently tend to forage intensively within a narrow patch, a behaviour especially typical immediately after a resource is discovered [184].

Standardised novel-object tests record contact latency, contact frequency, and changes in movement after the introduction of an unfamiliar stimulus [142]: latency captures when uncertainty becomes physical sampling, frequency captures repeated engagement, and movement change captures how strongly a familiar arena becomes uncertain again [166].

1.3.4 Fitness and ecological consequences

The behavioural differences described above have consequences beyond the individual encounter. Invasion biology increasingly treats aggression, exploration, and responses to novelty as reliable indicators of a species' invasive potential [147, 185].

Over longer timescales, both the heritable and the plastic components of behaviour feed into evolutionary trajectories [147]. Selection works directly on heritable behavioural traits [157], while plasticity plays a more unpredictable role — buffering populations against acute selective pressures in some cases, exposing them to novel pressures in others [163].

1.3.5 Anti-predator behaviour and escape responses

The link between visual appearance and actual encounters with predators is often gauged through anti-predator behaviours, particularly Flight Initiation Distance (FID; [186]), the distance at which an animal starts to flee from an approaching threat. It represents the optimal trade-off between the costs of fleeing (energy, lost foraging or mating time) and the perceived

risk of capture [186]. This trade-off is strongly influenced by visual appearance, especially how effective the animal's camouflage is in both colour and pattern [187]. Generally, more cryptic animals let predators get closer before they bolt, producing shorter FIDs [188]. This has been documented in birds [189] and in lizards, where FID is adjusted in real time according to how well concealed the animal perceives itself to be in its current setting [190]. Escape ability interacts with crypsis too: ectotherms at lower body temperatures — whose sprint speed may be impaired — tend to have longer FIDs to compensate [191]. Nevertheless, there are contradicting results. *Phrynosoma modestum*, for example, is so cryptic that it genuinely resembles a small stone, and when it is cool it actually allows closer approach — the opposite of the general ectotherm pattern — apparently gambling on immobility and exceptional background matching rather than a sprint [192]. That case shows how morphology, physiology, and behaviour can be co-adapted into an integrated anti-predator strategy, a point particularly relevant for the *Podarcis* species, whose dorsal patterning is a large part of why they are hard to spot.

Two refinements of Ydenberg and Dill's (1986) optimal-escape model address why escape decisions depend on more than the immediate approach. The asset-protection principle predicts that anti-predator effort varies with the value of what the animal currently holds, so that a higher-value resource raises the threshold for abandoning position [193]. The risk-allocation hypothesis predicts that anti-predator effort matches the temporal pattern of predation risk, with animals under chronic high risk allocating less effort to each individual event and animals under brief high-risk windows investing heavily within them [194]. Predators shape prey behaviour both through direct mortality and through the risk of predation itself: the perceived threat of a predator can suppress foraging, movement, and resource use even when no attack occurs, so-called non-consumptive or risk effects [195]. Because these effects operate continuously wherever predators are present, anti-predator behaviour is an ongoing cost that competes with foraging, thermoregulation, and social activity for an individual's time and attention. For ectotherms, access to suitable basking sites and warm microhabitats is itself a limiting resource: because body temperature governs performance, the ability to occupy and hold thermally favourable positions can be as important as access to food, and competition for these positions is a recognised axis of interaction among coexisting lizards [127].

Escape behaviour is described by three measures that capture different decision points. Flight initiation distance (FID) is the distance at which the animal abandons position and begins to flee [186]. Distance fled (FD) is how far the animal moves before stopping or entering refuge [196]. Hiding duration (HD), where measured, is the time spent inside refuge before re-emergence [197]. The three are not redundant: an animal can show short FID but long FD, or long FID and short HD, depending on local predation pressure, refuge availability, and thermal opportunity costs.

1.4 Visual signals: communication, camouflage, and their ecology

Whether a colour pattern conceals or reveals an animal depends on the visual system of the observer. Receiver-specific visual models compute chromatic and luminance contrasts using the photoreceptor sensitivities of a candidate viewer [198, 199]. A pattern that produces high chromatic contrast against a background under one model can produce low contrast under another, so receiver-specific modelling separates potential visibility to predators from potential signal availability to conspecifics.

1.4.1 Understanding visual signals in lizards

Visual signals in lizards mediate mate choice, social dominance, and predator avoidance [200, 201]. Functionally speaking, there are two main uses of animal visual signals: communication (mate choice, social hierarchy, warning displays/aposematic signalling, and mimetic displays) and survival (camouflage and thermoregulatory displays) [200, 202]. A common theme throughout this entire process is a continuous struggle between being noticeable to the correct audience while avoiding detection by the incorrect audience [202, 203]. This theme is obviously relevant to behavioural and morphological differences between *P. siculus* and *P. melisellensis* found in sympatric populations, where visual signals likely contribute to resource partitioning and interaction between the two species.

Animal colouration is referred to as the physical phenomenon of how light reflects off a surface [204]. As such, the three components of colouration (hue, saturation, and brightness) are measurable [204]. Each component of colouration varies greatly in many animals and is influenced by several factors including the sex, age of the animal, and season of the year [200]. *Podarcis* lizards are examples of animals showing great variation [128]. Visual systems vary greatly within taxonomic groups (for example, UV sensitivity is widespread) [201], and

variable environmental conditions affect the way any given signal is perceived by any observer [202].

The spatial distribution of colours across an animal's body, its colour pattern, is a component of the visual signal, separate from overall colouration [198, 201]. Patterns take many forms: spots, stripes, bars, blotches, mottling [198]. Their properties like the shape, size, number, orientation, spacing, regularity and connectivity of the elements vary between individuals independently of patch area, hue and intensity [201, 205], because the developmental processes that place pigment cells need not be those that decide which pigments are made or how much is laid down. In mammals, genes such as Agouti affect both, producing banded or patterned fur [206].

Research long concentrated on the quantity side of colouration, patch size and colour intensity [201]; pattern is now also treated as a signalling variable [205]. In birds, fish, insects and mammals, patterns indicate individual quality, condition, age, sex or species identity [205], and pattern complexity or symmetry can reflect developmental stability. Geometry has direct consequences too because disruptive patterns break up the body outline [207], and warning-signal arrangements appear shaped to make predators learn and remember unprofitable prey [208]. Because colour and pattern can be under different selective pressures, visual signals are often multi-component [200]. Lizard's overall colour may be shaped by the need to match the general background, while fine-scale patterning within it signals status to conspecifics or sharpens the match. Traits that serve predator avoidance and social interaction at once may influence competitive ability and facilitate niche partitioning and coexistence in sympatric *Podarcis*.

1.4.2 Factors affecting colour and pattern expression

What an animal looks like — how it is coloured and what marks are on it — is a result of the interaction of both internal (genetic) and external (dietary, environmental) factors to produce the different hues, saturations, intensities and spatial arrangements seen in animals [209].

Heritable colour and pattern variation provides the raw material on which selection can act [210, 211]. Specific genes and molecular cascades control pigment synthesis — e.g. MC1R within the melanocortin pathway [212] — as well as pigment deposition and the assembly of nanoscale architectures behind structural colours [210]. The spatial layout of coloured

elements is also genetically governed, with patterns arising from reaction-diffusion dynamics, cell-differentiation programmes, and similar developmental mechanisms [210]. Pleiotropic effects are common: genes that affect colouration and patterning also influence other systems [212]. MC1R-pathway signalling also modulates energy homeostasis, immunity, the stress axis, and aggressive behaviour, forging a link between external colour and internal state — what some authors call "signalling syndromes" [212]. Where multiple such loci sit close together on the chromosome, tightly linked gene clusters (or "supergenes") can maintain associations among colour, pattern, and behaviour [212].

In *Podarcis*, carotenoid-based pigments underlie mainly ventral colouration; the amount of carotenoid-rich food available limits the colour an individual can express [213]; separately, overall nutritional condition (including adequate protein intake) supports the structural components underlying colour expression and pattern definition [214]. In general, when an individual's nutritional status is poor, the quality and definition of the pattern decline, appearing faded or incomplete [205].

In condition-dependent signals, expression tracks the state of the individual [215]. Carotenoid-based colours behave this way, and so do properties of the pattern itself (intensity, completeness, symmetry) which only animals in good physiological condition express fully [214]. Hormones set much of the rest. Sex hormones produce most of the colour and pattern difference between males and females in the breeding season [205, 214], while glucocorticoids such as corticosterone suppress condition-dependent signals under stress [216, 217]. Age, social status, health and parasite load act in the same direction: older animals in better condition carry more complex, more sharply defined patterns [205, 212].

Colouration and pattern are also under heavy selective pressure from the external environment. Vision underpins object detection and recognition, navigation, mate assessment, and predator-prey interactions [218]. A habitat's visual properties — ambient light, spectral composition, structural complexity, background patterns — drive the evolution of both camouflage and signalling and often produce geographic variation in colour and pattern [202, 219]. Classic cases include the spot patterns and colours of Trinidadian guppies (*Poecilia reticulata*) [201], mosquitofish (*Gambusia affinis*) [220], and agamid lizards [221]. How well a colour or pattern works, whether for camouflage, warning, or sexual signalling [207, 222, 223], depends on its contrast against the background as the relevant observer perceives it

[199], across both achromatic and chromatic channels, which interact [224]. The scale and geometry of the background matter greatly to the evolution of cryptic patterning [225]. Ambient light matters most: its intensity and spectrum shift with habitat, time of day and cloud cover, changing how colours look and how far a signal carries [199, 202]. Under the green-yellow light of forest shade, selection favours different colours and camouflage patterns from those that work in the broad-spectrum light of open ground [202].

Predation is among the strongest selective forces acting on colour and pattern, and its effect usually pushes animals toward resembling their backgrounds in both colour and spatial pattern [226]. The effectiveness of crypsis is environment-dependent, and the resulting strategies span a spectrum from broad generalists to narrow specialists [207]. Camouflage also carries costs: dense vegetation may shield an animal from predators yet simultaneously hamper thermoregulation [227] and reduce its visibility to potential mates. Because pattern-dependent camouflage so often pulls against thermoregulatory needs and intraspecific signalling, many organisms manage this conflict by partitioning their signals spatially — restricting bright or conspicuous markings to certain body regions and keeping everything else cryptic [203]. Both study species resolve the conflict between concealment and signalling with spatial segregation, a cryptic dorsum and a flank that carries blue ventrolateral patches that a rival sees at close range and a bird overhead does not [203, 228]. *P. melisellensis* adds discrete ventral colour morphs, so the cost of conspicuous colour falls on part of the population only [128, 129]. In seasonally shifting environments (snow cover, leaf-litter turnover), some species take this a step further and express wholly different colour phenotypes across the year; the arctic hare and its shift from mottled brown summer pelage to white winter coat is one well-known case [229].

For *P. siculus* and *P. melisellensis*, these environmental pressures ought to generate locally adapted differences in anti-predator colouration and patterning — differences that could separate the two species even where they live in syntopy. How active each species is and which microhabitats it prefers may well be linked to cryptic colour and pattern variants — dorsal striping or reticulation, for instance — as well as to how conspicuous each species is to predators, which in turn affects flight-initiation distances and, ultimately, coexistence [230, 231]. In addition, anthropogenic changes — pollution, habitat destruction, artificial light, climate change — are altering animal colour and pattern expression [232]. For *Podarcis* specifically, such anthropogenic effects on colouration have not yet been documented. Other

sources of variation in expression are, however, well documented within the genus: dorsal-pattern morphs differ among *P. siculus* populations [131], and *P. melisellensis* maintains discrete ventral colour morphs [128], so both pattern and colour expression vary within these species at the population level.

1.4.3 Colours and patterns in communication

Colouration and pattern together function as communication tools in animals, mediating interactions both within and between species. They carry information about the sender's identity, condition, quality, or intent, and they shape receiver behaviour in ways that, on balance, benefit the sender [233].

Social interaction gives the clearest examples. Patterns help animals establish and maintain a rank in the hierarchy and settle a contest without fighting [205] — what ethologists call a badge of status [234]. Such badges are conspicuous and easy to read: bright skin patches, or sharply defined elements such as spotted bibs, facial stripes and flank bars, which advertise status, dominance or willingness to fight [235]. The fine detail carries the information: the spacing of spots in a bird's bib [235] and the width of stripes in a cichlid [236] both predict fighting ability. In several lacertids, the blue lateral spots along the flanks may work the same way, advertising dominance or fighting capacity to conspecifics.

Lizards are among the best-studied groups in this regard. The throat of *Urosaurus ornatus* can show blue/orange combinations with spots, and these markings predict dominance status, aggressiveness, reproductive tactic, and locomotor capacity [237]. In *Platysaurus broadleyi*, UV reflectance off a specific throat patch provides a reliable readout of fighting ability and territory ownership [238]. For *P. muralis*, the count and spatial arrangement of black ventral spots — a discrete pattern trait — turn out to be a stronger predictor of contest outcome than overall throat colour [239]. In *Tropidurus semitaeniatus*, a chest region where dark pigmentation and yellow chroma combine into a mottled look — signal dominance, influence whether opponents act aggressively or evasively and predict contest outcomes [228]. Even the relatively simple red ventral colouration of *Intellagama lesueurii* works as an aggression or intimidation signal during male contests [240]. Whether *P. siculus* and *P. melisellensis* differ in signalling traits — blue flank spot prominence, ventral spot patterns, and so on — is not yet known.

Species recognition through visual signals — often involving species-specific patterns like unique stripe configurations, head markings, or distinctive dewlap patterns — is especially important in sympatry, where it guards against costly hybridisation [241]. *Anolis* lizards, for instance, pair species-specific head-bobbing displays with dewlaps whose colour and pattern contribute to recognition [242]. Recognition cues of this sort probably involve a combination of pattern, colour, and movement [218].

Some of the changes to the trait can be attributed to sensory exploitation; as some signalers will develop traits because those traits take advantage of existing sensory biases of receivers [243] rather than providing the receiver with information about the signaler. For example, a male Túngara frog call including "chucks" may have evolved to exploit female sensitivity to auditory stimuli [243]. An analogous mechanism may also be present for visual signals – i.e., preference by receivers for certain geometric characteristics (e.g., symmetry or specific spatial frequencies) of patterns. A few visual characteristics are multi-purpose and thus serve several functions. The throat colouration and patterning in *U. ornatus*, for instance, is used as both a status indicator in male-male interactions and as an intersex cue during mate selection [237]. This results in a 'tangled' selective landscape when the phenotype that is selected for in one context is not optimal in another [231].

1.4.4 Colour and pattern in survival

Visual appearance affects survival through several partially competing channels, among them camouflage, warning colouration, and thermoregulation [200, 210, 244].

Crypsis is the most rudimentary type of camouflage — when the animal is completely undetected [245]. The most frequent form of this is background matching, when an animals' colouration, pattern elements, brightness and texture are as close as possible to the overall visual characteristics of their environment [207]. Decreasing the signal-to-noise ratio until the animal is statistically indistinguishable from its immediate surroundings results in camouflage [245]. Classic examples include moths resting on tree bark, cuttlefish matching the seabed, and lizards with dorsal patterns that resemble rocks or dry leaves [207].

For background matching to be successful, the animal must mimic their substrate in multiple visual parameters simultaneously — i.e., the scale, shape, and spacing of individual pattern elements vis-a-vis the background [225]. Disruptive colouration works with a different

strategy; high-contrast markings (i.e., patches, stripes, spots, etc.) of greatly differing brightness or colour that disrupt the animal's apparent boundaries and features [204]. These markings cause false outlines and usurp the edge-detecting circuits of a predator's eyesight; since many of them span the animal's real boundaries, they hinder the predator's detection and identification of the animal [246]. Examples of such markings include leopard "rosettes", zebra stripes, insect wing patterns, and military camouflage [247].

Countershading (Thayer's Law) involves a darker dorsal surface grading into a lighter ventral one [248]. The strategy is common, the gradient compensates for self-shadowing from overhead light, flattening the appearance of three-dimensional form and making the animal less conspicuous [248]. Though countershading is primarily about shading gradients, subtle patterning of the countershaded areas can improve the overall effect. Another phenomenon is masquerade: the animal is detected, but the predator misidentifies it as something inedible or uninteresting — a leaf, a twig, a stone [247]. It works through cognitive misclassification: the animal shares enough visual features with an inedible model to fool the predator [187], e.g. stick and leaf insects, twig-mimicking caterpillars, and leaf-tailed geckos [247]. Masquerade is related to, but distinct from, protective mimicry. A mimic resembles another organism, typically a defended or unpalatable model, and exploits the receiver's learned or innate response to that organism, whereas a masquerading animal resembles an inedible object and is misclassified as uninteresting rather than avoided [247]. These camouflage strategies, many of them pattern-dependent, target different stages of the predator's perceptual pipeline [245]. Which strategy best suits a given species depends on its habitat, behaviour, and the sensory abilities of the predators it faces. The effectiveness of camouflage — colour matching and pattern matching to microhabitat alike — in *P. siculus* versus *P. melisellensis* remains an open question.

Behaviour frequently amplifies the effects of morphological camouflage [221]. Animals go out of their way to rest on substrates where their markings and textures are a good match, a phenomenon called background selection or background choice. How the body is oriented also matters — an animal can line up its pattern elements with features of the background (stripes parallel to grass blades, for instance) or angle itself to get the most out of countershading. Immobility also matters, since even effective crypsis fails once the animal moves [221]. In colour-changing species like chameleon prawns, behaviour and physiology cooperate to maximise concealment [249]. Communication signals show the same coupling,

often requiring display behaviours to reveal, position, or orient a pattern toward its intended receiver [240]. Selection therefore acts on the integrated phenotype. Evolutionary change in colouration or pattern can demand corresponding behavioural shifts, and vice versa, so differences in dorsal or lateral patterning between *P. siculus* and *P. melisellensis* may have evolved hand in hand with anti-predator behaviours or microhabitat preferences [221].

Aposematic species work on the opposite principle. Instead of concealment, they broadcast loud, high-contrast signals — vivid colours in bold, repetitive spatial motifs (the spots of ladybirds, the bands of wasps) — that warn would-be predators of toxicity or defensive weaponry [222]. These warning signals and their associated patterns aid predator learning: a single bad experience can be enough for a predator to avoid similarly patterned prey in the future. To be effective, a warning signal must be easy to detect and easy to remember. Larger and brighter signals reinforce avoidance learning and are more readily memorised, and internal contrast boundaries raise the salience of the signal and improve survival even where overall conspicuousness is low [250]. Predators then generalise their learned avoidance to prey sharing the model's colours, which is what favours convergence on similar warning patterns [251]. Predator psychology — innate biases and learning ability alike —shapes the evolution of aposematic signals [222]. Even though there is strong selection for uniformity (a clear, unambiguous signal), warning signals and patterns do vary within and among populations, probably because of fluctuating predation pressures, genetic constraints, gene flow, or conflicting selection from other sources [252].

There is also a direct thermal dimension to colouration and, to a lesser extent, pattern. The ratio of dark to light surface area determines how much solar radiation an animal absorbs, which matters greatly for ectotherms [253]. Dark surfaces absorb more heat; light ones reflect it more [254]. Simple physics can push selection toward different colour morphs or patterning variants depending on the local thermal regime — melanistic dorsal striping, for example, might produce a mosaic of warmer and cooler zones on the body surface — and it can also drive seasonal colour shifts within a single species [255].

1.5 Rationale, objectives and hypotheses

The two species differ sharply in range and status. *P. siculus* is one of Europe's most successful invasive reptiles [117, 119]; *P. melisellensis* is endemic to the Adriatic. They now

share large parts of the Adriatic archipelago, and where they meet, *P. siculus* usually gains ground [9, 102, 109, 117, 132]. What happens is therefore well documented; how it happens is not. Direct interference could enable that. In staged encounters *P. siculus* is the more aggressive of the two and displaces *P. melisellensis* from preferred basking sites [9]. Whether it behaves the same way in the wild is unknown, because no one has compared the two in syntopy.

P. melisellensis is more closely tied to drystone walls and other structurally distinct microhabitats than the generalist *P. siculus* [101]. Under the neophobia threshold hypothesis, aversion to novelty acts as a proximate brake on niche expansion, so that habitat generalists are less neophobic than habitat specialists [256, 257]. *P. siculus* is therefore expected to show the weaker neophobic response. Because exploration and neophobia arise from separate motivations, greater exploration in *P. siculus* is treated here as a related prediction rather than the same one.

Colour influences crypsis, and crypsis is in turn shaped by behaviour. An animal displaying good camouflage may be able to remain stationary while a predator approaches, whereas a conspicuous animal may need to flee earlier or rely upon active defence. If the two species differ in the degree of conspicuousness of their lateral signalling traits, as expected, that difference should carry over into the anti-predator tactics they use, including flight initiation distance, immobility, and escape frequency. Whether it does so in sympatric contexts is also currently unknown.

P. melisellensis may signal dominance via ventral colouration despite rarely escalating to fighting. The behaviours the two species display during intra- and interspecific interactions remain to be characterised.

A pattern of trait differences between species is consistent with adaptive divergence but does not on its own demonstrate that selection produced the pattern [258]. Stable species differences can also reflect developmental constraints or historical contingency [258], and apparent differences can arise from plastic responses to the animals' current environments rather than from evolved divergence; where this has been measured across populations, plasticity often explains more of the observed divergence than genetic differentiation does

[259]. Accordingly, the *P. siculus* / *P. melisellensis* differences reported here are interpreted cautiously, as candidate adaptive divergence rather than demonstrated selection.

Therefore, the research conducted in this thesis will provide value for several reasons. If *P. melisellensis* is being excluded by behavioural interference, then conservation efforts will need to take into consideration this mechanism, rather than simply considering habitat loss. If the two species are partitioning resources behaviourally — e.g., exhibiting different exploration styles, activity patterns or micro-habitat uses — then coexistence of the two species may be more stable than the previously discussed dominance hierarchies suggest. Lastly, if colouration is linked to both crypsis and signalling, then morphological divergence may represent the influence of multiple selective pressures acting simultaneously.

1.5.1 Objectives

The main objective of this thesis is to assess behavioural divergence between *P. siculus* and *P. melisellensis* populations coexisting in sympatry. A secondary objective is to identify morphological traits consistently associated with behaviour within and between species. Throughout, colouration, pattern, and behaviour are treated as one functional set and compared between the two species.

Competition does not act on single traits in isolation: behavioural and morphological traits that respond to the same ecological problem can form a functional set [260, 261]. A functional grouping is defined by shared task, not by shared developmental or genetic pathway, and is therefore distinct from phenotypic integration in the strict sense, which requires within-individual covariance and a common developmental or genetic architecture [262, 263]. The distinction matters when traits are compared between species rather than within individuals.

1.5.2 Hypotheses

H1. *P. melisellensis* will show lower exploration and higher neophobia than *P. siculus*.

H2. *P. melisellensis* will have less conspicuous dorsal and lateral colouration (better crypsis) and will express lower levels of anti-predatory behaviour than *P. siculus*.

H3. *P. melisellensis* will display more intense dominance signalling colouration but lower aggression in intra- and interspecific encounters than *P. siculus*.

2. Materials and Methods

2.1 Study animals and field procedures

Adult lizards of the Italian Wall Lizard (*Podarcis siculus*, PS) and the Dalmatian Wall Lizard (*Podarcis melisellensis*, PM) were used in this study. Animals were captured by hand or noose during late summer to early autumn (September to October) across two consecutive years, 2020 and 2021. Fieldwork was conducted near Knin (approx. 44.0418° N, 16.2329° E), Pag (approx. 44.5686° N, 14.8902° E), and Sinj (approx. 43.7226° N, 16.6738° E), Croatia (Figure 1). I selected these locations because both species occur at each site in sympatry and syntopy. The sites are separated by at least 50 km, so they were treated as distinct sampling locations. They consist of comparable habitat complexity, including agricultural fields, pastures, and meadows interspersed with hilly terrain featuring macchia and forest patches. The sites are not identical climatically. Sinj and Knin are submediterranean, whereas Pag is transitional between submediterranean and mediterranean conditions. This difference influences vegetation. Sinj and Knin share similar submediterranean plant communities (characterised by species such as *Quercus pubescens*, *Carpinus orientalis*, and *Juniperus oxycedrus*), whereas Pag additionally incorporates Mediterranean elements such as *Quercus ilex*, *Spartium junceum*, and *Phillyrea angustifolia* within its macchia. Quantitative data on predator abundance, predation pressure, refuge use, and food consumption have not been studied for these specific locations. Habitat structure and vegetation were characterised qualitatively only and were not quantified.

Figure 1. Map of the three field research locations (Knin, Pag, Sinj) in the Eastern Adriatic mainland and on the island of Pag.

The following procedures were identical for both cohorts (2020 and 2021), unless indicated otherwise. I quantified anti-predator behaviour in the field immediately upon detecting a lizard, before any capture attempt. A single researcher approached the focal animal while maintaining consistent attire and a standardised, slow approach velocity. I recorded three metrics: flight initiation distance (FID), defined as the distance between the researcher and the lizard at the moment escape was initiated; flight distance (FD), defined as the distance the lizard fled before stopping; and hiding duration (HD), defined as the time the lizard spent concealed if it entered a refuge, observed until re-emergence up to a maximum of 300 s (Table 1). Across both years, I recorded these field behaviours for a total of 451 individuals. Colouration (JND) data were obtained for a balanced subset of 60 of them, five males and five females of each species at each location, so the species-specific models that include visual contrast components (Tables 4 and 5) are each fitted on 30. Both samples are given by location, species and sex in Table S26. Only after completing these observations were lizards captured for the laboratory study.

Table 1. Field anti-predator behaviour variables recorded during the approach test upon detecting a lizard.

Variable	Unit	Definition / measurement
Flight initiation distance, FID	cm	Distance between the approaching researcher and the lizard when escape was initiated.
Flight distance, FD	cm	Distance the lizard fled before stopping.
Hiding occurrence	–	Whether the lizard entered a refuge after escape.
Hiding duration, HD	s	Time spent hidden after entering a refuge, observed until re-emergence up to a maximum of 300 s.

A total of 240 lizards were used for the laboratory components of the study. Of these, 230 completed the full round of laboratory testing; the remainder were lost to deaths or escapes during husbandry and were excluded from the laboratory analyses. Each year, 10 males and 10 females of each species were collected at each of the three locations, giving 120 lizards per year. Sex was determined from external characteristics and body shape, with males showing distinct femoral pores and a swollen tail base [113]. Individuals whose sex could not be determined, as well as juveniles and sub-adults, were released immediately and not included in the study.

All procedures complied with the Animal Protection Act (NN 102/17, 32/19), the Ordinance on the Protection of Animals Used for Scientific Purposes (NN 55/13, 116/19), and the ASAB/ABS guidelines for the ethical treatment of nonhuman animals in behavioural research and teaching [264]. The study protocol was approved by the Ethics Committee of the Faculty of Science, University of Zagreb (Klasa: 641-01/19-01/39; ur. br.: 251-58-10617-19-3). Research permits for fieldwork and capture of the strictly protected species *Podarcis melisellensis* were issued by the Ministry of Economy and Sustainable Development for 2020 (Klasa: UP/I-612-07/20-48/121; ur. br.: 517-05-1-1-20-6) and 2021 (Klasa: UP/I-612-07/21-

48/202; ur. br.: 517-10-1-1-21-4). Additional ethical approval for the doctoral experiments was issued separately (Klasa: 643-02/21-01/1; ur. br.: 251-58-10617-21-1).

2.2 Laboratory husbandry and acclimatisation

Once captured, lizards were transported to the Reptile facility at the Division of Animal Physiology, Department of Biology, Faculty of Science, University of Zagreb, Croatia (HR-POK-027). Upon arrival, the lizards underwent a one-month acclimatisation period before behavioural testing. Lizards were not weighed or measured during the acclimatisation period, and body measurements were taken only after completion of behavioural testing. Each lizard was individually housed in a plastic terrarium (approx. 40 L × 30 W × 30 H cm) equipped with peat substrate, a hiding spot (shelter), and constant access to water. A heat bulb positioned above a rock at one end of each terrarium created a thermal gradient for thermoregulation. A separate Arcadia ProT5 UV-B kit (D3 Forest 6% UVB, 54 W / 1150 mm and 39 W / 850 mm; Arcadia, United Kingdom) was installed to provide 6% UVB and 30% UVA radiation, imitate natural sunlight, and support vitamin D3 synthesis and calcium metabolism. The facility simulated natural light cycles (12 hours light: 12 hours dark) and maintained temperature conditions appropriate for the season (approx. 22°C at night; 25°C base temperature during the day).

Lizards were fed live crickets (*Gryllus assimilis*) every other day, enriched with calcium and vitamins every other week. Plastic tubes were placed within each terrarium to minimise handling stress during transfers to and from experimental setups. The tubes also functioned as a familiar refuge and transfer device [265]. Following the completion of all behavioural testing and measurements, animals were humanely sacrificed for use in a separate study [266, 267].

2.3 Laboratory behavioural testing

Testing took place between 09:00 and 17:00 hours [107] under controlled temperature conditions, detailed below for each test. To establish an unbiased testing sequence, the order for all 120 individuals per year was initially randomised based on their species, sex, and location using an online tool (www.randomizer.org). However, due to the large number of animals, testing was conducted in manageable batches, each cohort of 120 lizards was divided

into four balanced testing groups: three groups of 32 individuals and one group of 24 individuals. Each group was moved to the behavioural testing room and completed the full test sequence within one week. Within each group, the randomised order was retained across tests. Care was taken to ensure that each of these testing groups remained balanced with respect to species, sex, and location representation. Within each of these testing groups, the pre-determined randomised sequence for those specific individuals was then strictly followed across the different testing sessions. This two-step procedure (overall randomisation followed by consistent sequencing within balanced logistical groups) ensured that while the fundamental order was random, the relative timing between tests and the order experienced relative to immediate cage neighbours was kept consistent for all individuals processed within the same batch.

Multiple parallel experimental setups, including four arenas for open field tests, were used simultaneously to increase throughput. After each trial, test chambers were thoroughly cleaned with 30% ethanol to remove residual odours or chemical cues [268, 269]. All behavioural trials were recorded using video cameras mounted above the arenas for later analysis. Video analysis was performed using Noldus EthoVision XT 15 software (Noldus Information Technology, Wageningen, Netherlands), which automatically tracked lizard movement and supplied the movement variables (number of moving segments, distance moved, movement duration, and angular velocity). The agonistic variables were not obtained by automated tracking: displays, chases and lunges, bites, and the latency to the first aggressive act were scored manually from the same video recordings by a single observer, following the fixed ethogram given in Table 2.

2.3.1 Exploratory behaviour and neophilia/neophobia

I evaluated exploratory behaviour and responses to novelty through an Open Field Test (OFT) [133]. This test involved placing individual lizards into an empty, non-transparent Plexiglas open-top box (50 × 50 × 50 cm) maintained at a consistent temperature of 30°C. Animals were transferred from their home terrariums into the arena using the plastic tube from their terrarium and gently coaxed to exit; the tube was then immediately removed. Each trial lasted 15 minutes and was video recorded. At the end of each trial, the lizard was guided back into its tube and returned to its terrarium.

Each lizard was subjected to a standardised behavioural assay spanning two consecutive days, consisting of four 15-minute open field trials. On the first day, individuals completed two consecutive trials: an initial exposure to the novel arena to assess exploration behaviour (Context 1: Novel Environment Test), followed by a second exposure intended for habituation to the testing environment. On the second day, lizards underwent two additional trials: a third exposure to the now-familiar arena to evaluate activity levels (Context 2: Familiar Environment Test), and a fourth trial in which a novel object, a small knotted piece of powder-free rubber glove, was placed centrally within the arena to assess neophilia/neophobia (Context 3: Novel Object Test).

The same four movement-related variables were extracted from video tracking in the exploration, activity, and neophilia trials: number of moving segments, distance moved, movement duration, and angular velocity (°/s). Direct interaction with the novel object was scored manually from video playback as contact latency and contact frequency. Contact latency was defined as the time from the start of the trial until the lizard first made physical contact with the object; individuals that never contacted the object were right-censored at the 900 s trial maximum. Contact frequency was defined as the total number of discrete contacts initiated by the lizard; if continuous contact occurred, a new contact was tallied every 5 seconds. Neophobia was calculated as the log-ratio between the neophilia trial and the activity trial for each movement-related variable. A complete list of measured behavioural variables is summarised in Table 2.

2.3.2 Aggression

Following the completion of exploration tests, aggressive interactions were assessed using dyadic encounters staged within the same 50 × 50 × 50 cm arenas, modified with an opaque divider initially separating the two lizards. The behavioural room was precooled night before the trial so that all trials began under the same temperature conditions, and the room was maintained at 20°C during testing. A single heat source was positioned at the centre of the arena to encourage interaction over this thermal resource once the divider was removed. After divider removal, behaviour was recorded for 10 minutes.

Each lizard was tested once in a conspecific, within-species encounter and once in a heterospecific, between-species encounter. All pairings consisted of sex-matched individuals

from different sampling locations, so paired individuals were unfamiliar. Intraspecific testing was conducted on Wednesdays and interspecific testing on Fridays, allowing for a 48-hour resting period between aggressive testing sessions. This interval was chosen to minimise carry-over of fighting experience [84]. In a lizard contest experiment, winner–loser effects of a previous contest were no longer detectable after such a gap [270]. For within-species pairings, individuals were matched based on similar snout-vent length (SVL), following the size-matching protocols standard in staged lizard contests [271, 272, 273], to minimise size asymmetrical effects within species. Due to the inherent size disparity between *P. siculus* and *P. melisellensis*, between-species encounters paired individuals based on their relative size ranks within their respective species samples, for example the largest *P. melisellensis* male was paired with the largest *P. siculus* male, the second largest with the second largest, and so on. This method aimed to make between-species encounters comparable by controlling for relative, rather than absolute, size differences.

Variables scored from aggression trials included aggression occurrence, latency to the first aggressive act, the number of displays, chases/lunges and bites, the mean distance of each focal lizard from the centre of the arena, and the mean distance between the two interacting lizards. Aggression occurrence was treated as a binary variable (scored 1 if at least one display, chase/lunge, or bite occurred during the trial, 0 otherwise). Chases/lunges and bites were treated as more escalated aggressive behaviours. If a prolonged bite occurred, a new bite was counted every 5 seconds. Aggressive acts were grouped into three escalating categories — displays (lowest intensity), chases/lunges (medium intensity), and bites (highest intensity) — so that the intensity of aggression is reflected in the type of act performed.

Table 2. Behavioural variables measured in laboratory tests.

Type of behaviour	Test environment	Variables scored from videos	Definition
Exploration	New (first exposure to the empty arena)	Distance moved (cm)	Total distance the animal moved during a trial.
		Movement duration (s)	Amount of time the animal spent moving during a trial.
Activity	Familiar (after previous exposure to the arena)	Number of moving segments	Number of times the animal started moving during a trial.
		Angular velocity (°/s)	Rate of change in direction of the lizard's movement during a trial.
Neophilia	Familiar + novel object	Latency to contact the novel object (s)	Time from the start of the trial until the lizard first makes physical contact with the novel object.
		Frequency of contact with the novel object	Number of contacts with a novel object during a trial.

Type of behaviour	Test environment	Variables scored from videos	Definition
Neophobia	Derived metric	Distance moved (cm), movement duration (s), number of moving segments, angular velocity (°/s)	Calculated as log (novel object environment / familiar environment) for each of these four behavioural variables.
Aggression	Dyadic encounters	Aggression occurrence	Binary – occurred or not
		Aggression type: displays; chases/lunges; bites	Type of aggressive behaviour
		Latency to first aggressive act	Time from divider removal to the first display, chase/lunge, or bite. Trials without aggression within 600 s were treated as right-censored.
		Distance from centre	Mean distance from the arena centre.
		Inter-individual distance	Mean distance between the two lizards.

2.4 Post-behavioural measurements: morphology, colouration, and pattern

All morphological measurements, pattern photography, and spectrometry were conducted after all individuals had completed the full sequence of behavioural tests described above. This reduced the chance that handling stress from physical measurements influenced behavioural results.

2.4.1 Morphological measurements

Standard morphometrics were assessed consistently by a single researcher using a digital caliper (±0.1 mm). Measurements included SVL, interlimb length (ILL), limb lengths (forelimb and hindlimb), head width (HW), head length, head height, jaw length, jaw outlever, and snout length. All length measurements were taken on the lizard's right side for paired structures (limbs, ILL) and for head dimensions. Body mass was recorded using a digital scale (±0.1 g, Soehnle) on the same day as morphometric measurements. From these primary measurements, I calculated the interlimb ratio (ILL/SVL), the hindlimb-to-forelimb ratio (Right Hind LL / Right Front LL), and the Scaled Mass Index (SMI) following the methodology of Peig and Green [274]. Size-corrected residual morphometrics were derived by regressing log-transformed head and jaw dimensions against log-transformed SVL, providing size-independent shape variables for subsequent analyses. Descriptive statistics for these measurements, by species, sex and location, are given in Table S24.

2.4.2 Colouration measurement

Spectral reflectance was measured in the laboratory on 60 individuals, five males and five females per species per site, randomly selected from the 2021 cohort after they had completed all behavioural tests. An Ocean Optics USB2000 spectrophotometer connected via a 1.2-metre bifurcated fibre optic probe to a PX-2 pulsed xenon light source was used. Measurements were standardised using a probe holder that maintained a 90° angle relative to the surface and a consistent distance of 2 to 3 mm, resulting in a measurement spot of approximately 3 mm diameter while excluding ambient light. All reflectance measurements were taken relative to a certified 99% white reflectance standard (Labsphere, North Sutton, NH, USA).

Measurements were collected from standardised body regions: the upper back, corresponding to the predominantly green area near the head base; the lower back, corresponding to the predominantly brown area near the tail base; the right flank; and ventral regions, including the throat and belly. Distinct melanic patches or irregularities were avoided. Two measurements were taken per region and subsequently averaged for analysis. To assess colour signals relevant to intraspecific signalling, two distinct flank regions were measured separately: the blue UV-reflective spots and the surrounding brown flank background.

To characterise the visual background in which the animals naturally occur, spectral reflectance was also measured from habitat background components, including stone, grass, leaf litter, anthropogenic materials, bare ground, and branches. Representative samples of each component were collected at the study sites and measured in the laboratory under the same conditions as the lizard measurements. Reflectance was measured 20 times for each of 25 different background samples. For visual modelling, these spectra were averaged to create six reflectance-based habitat background components: stone (n = 5 backgrounds averaged), grass (n = 4), leaf (n = 3), anthropogenic (n = 5), ground (n = 5), and branch (n = 3).

Spectral reflectance data were processed using the pavo package in R [275]. Spectra were visualised and quality-checked, negative reflectance values resulting from electrical noise were adjusted using procspec with fixneg = "addmin", and spectra were smoothed using opt = "smooth" and span = 0.2. Visual modelling was performed using receptor-noise-limited models [199]. Model outputs were expressed as Just Noticeable Differences (JNDs), which estimate perceptual contrast between two spectra for a defined visual system. Chromatic contrast (dS) describes colour contrast based on cone photoreceptor channels, whereas luminance contrast (dL) describes achromatic brightness contrast. For avian and *Podarcis* visual models, luminance contrast was calculated from the double-cone signal, which is commonly used as the achromatic channel in receptor-noise-limited models.

Two visual modelling approaches were applied. First, visibility to predators was estimated by comparing lizard body regions with the six reflectance-based habitat background components described above. These contrasts were calculated using visual system parameters for potential avian predators (Blue Tit average UVS model) [276] and serpentine predators (Garter snake trichromatic model) [277], adapting approaches from Stuart-Fox et al [278]. Second, blue flank spot conspicuousness was estimated by comparing the blue UV-reflective flank spots

with the surrounding brown flank background using a *Podarcis*-specific tetrachromatic visual model with sensor sensitivities set at 367, 456, 497, and 562 nm. For this model, JNDs were calculated using a Weber fraction of 0.05, and luminance contrast was calculated from the double-cone signal.

2.4.3 Dorsal pattern measurement and analysis

Digital photographs capturing dorsal patterns (135 photographs in total) were taken after behavioural testing under standardised conditions, including consistent camera settings, lighting, distance, angle, and inclusion of a ColorChecker target. Images were excluded from analysis if the lizard bore conspicuous physical markings from aggression tests or if photograph quality was compromised by significant overexposure. A post-processing workflow was used to standardise colour, including RAW to DNG conversion, custom calibrated camera profiles, and Photoshop harmonisation guided by ColorChecker values.

Two distinct analytical approaches were applied to these dorsal pattern images. The first approach aimed to explore overall dorsal pattern variation and identify general differences between predefined groups, including species, sex, and location, independent of specific background comparisons. For this unsupervised pattern analysis, complex, high-level pattern features were extracted from the standardised dorsal images using a pre-trained ResNet50 Convolutional Neural Network (CNN) via PyTorch [279] and the associated torchvision library, adapting methods from Puissant et al [280]. Standard image preprocessing, including resizing, tensor conversion, and normalisation based on ImageNet statistics, was applied before feeding images to the network. Feature vectors summarising the pattern were obtained from the activations of the network's final global average pooling (GAP) layer. In CNNs such as ResNet50, layers progressively extract more complex features, culminating in spatial feature maps before the classification layers. GAP reduces each final feature map to a single value by averaging across its spatial dimensions, creating a fixed-size vector that summarises the presence and intensity of high-level features, such as learned patterns, textures, and shapes, across the entire image. I used this fixed-size vector as the quantitative input for multivariate analysis.

The second analytical approach aimed to quantify camouflage effectiveness by comparing each lizard's dorsal pattern against representative natural backgrounds. For this purpose,

photographs were taken of natural backgrounds where lizards were typically observed in the field, using the same standardised height and including the ColorChecker target as for the lizard photos. Image sections were extracted from these background photos, matching the average aspect ratio of the lizard dorsal pattern regions. These background image patches were assigned to six categories: anthropogenic, vegetation, stone, bark, ground, and complex.

Quantitative comparison between lizard dorsal images and background image patches was performed using Python (v3.9) libraries, including OpenCV, Scikit-image, Pillow, NumPy, and Pandas. Images were resized to 320 × 320 pixels using Lanczos resampling. This interpolation method was chosen because it preserves image sharpness and detail while minimising aliasing artefacts compared to simpler methods, especially during image downscaling [281].

Three complementary metrics quantified visual differences, adapting methodologies from Bai et al [282]. First, the Image Color Similarity Index (ICSI) quantified colour differences. Images were transformed into the device-independent CIE XYZ colour space, followed by conversion to the CIELAB colour space, which is designed to be perceptually uniform. Spatial filtering analogous to S-CIELAB was applied via independent Gaussian blurring (σ = 1, 2, 4 pixels) of the L*, a*, and b* channels. The pixel-wise Euclidean distance (ΔE) map between filtered lizard and background images was computed for each scale, and the ICSI value was calculated as the standard deviation of this distance map, averaged across the three scales.

Second, Gradient Magnitude Similarity Deviation (GMSD) [283] assessed differences in structural information. Images were converted to greyscale and subjected to multi-scale Gaussian blurring (σ = 1, 2, 4 pixels). Gradient magnitudes were computed using a 3 × 3 Sobel operator. The gradient magnitude similarity (GMS) map compared local gradient strengths between images, and the GMSD for each scale was calculated as the standard deviation of the GMS map, averaged across scales.

Third, Local Binary Patterns (LBP) [284] captured texture differences. Greyscale images were processed using the uniform LBP variant, with eight sampling points and a radius of one pixel, to generate histograms characterising the distribution of local patterns, including spots,

edges, and flat areas. Texture dissimilarity was calculated as the Chi-squared distance between the normalised histograms of the lizard and background images.

For each lizard against each background image category, average ICSI, GMSD, and LBP scores were calculated by averaging across all background patches within that category. These average component scores were normalised to a 0-1 range within each background category using min-max scaling. Entropy-based weights were calculated from the distribution of normalised component scores across individuals within each background category. Thus, the weighting describes the relative contribution of each metric to among-individual differences for a given background category, rather than variation within a single lizard image. Because the component metrics originally measured dissimilarity, normalised values were inverted before calculating the final composite score. A final composite camouflage score was then calculated for each lizard-background pairing as the weighted sum of the normalised component scores. Higher composite camouflage scores indicate a better visual match between the lizard dorsum and the corresponding background category. All colour, visual-contrast, and dorsal-pattern variables entering these analyses are summarised in Table 3.

Table 3. Colour, visual-contrast, and dorsal-pattern variables used in visual modelling and image analyses.*

Measurement group	Variable	Measurement / comparison	Definition / measurement
Spectral reflectance	Lizard reflectance spectra (%)	Upper back, lower back, flank, throat, belly, blue flank spot, and surrounding brown flank background	Spectral reflectance measured from standardised lizard body regions.
	Habitat background reflectance spectra (%)	Stone, grass, leaf litter, anthropogenic material, bare ground, and branches	Spectral reflectance measured from habitat components used as visual backgrounds.
Modelled visibility to predators	Chromatic contrast, dS	Lizard body regions compared with habitat background components using bird and snake visual models	JND-based estimate of colour contrast between the lizard and the background.
	Luminance contrast, dL	Lizard body regions compared with habitat background components using bird and snake visual models	JND-based estimate of brightness contrast between the lizard and the background.
Intraspecific signalling	Blue-spot chromatic contrast, dS	Blue flank spot compared with surrounding brown flank background using the *Podarcis* visual model	JND-based estimate of chromatic conspicuousness of the blue flank spot to conspecifics.
	Blue-spot luminance contrast, dL	Blue flank spot compared with surrounding brown flank background using the *Podarcis* visual model	JND-based estimate of luminance conspicuousness of the blue flank spot to conspecifics.

Measurement group	Variable	Measurement / comparison	Definition / measurement
Dorsal camouflage	Image Color Similarity Index (ICSI)	Dorsal images compared with background image categories	Colour-difference metric used to estimate dorsal colour matching.
	Gradient Magnitude Similarity Deviation (GMSD)	Dorsal images compared with background image categories	Structural-difference metric based on gradient information.
	Local Binary Pattern (LBP) distance	Dorsal images compared with background image categories	Texture-difference metric based on local binary patterns.
	Composite camouflage score	Dorsal images compared with anthropogenic, vegetation, stone, bark, ground, and complex backgrounds	Weighted composite of colour, structure, and texture matching. Higher values indicate better visual matching to the background.
Dorsal pattern variation	ResNet50 feature vectors	Standardised dorsal images of individual lizards	Deep-feature representation of dorsal pattern.
	Principal components	Principal components derived from ResNet50 feature vectors	Reduced-dimensional representation of dorsal pattern variation used for visualisation and group comparisons.

*Visual contrasts are expressed as Just Noticeable Differences (JND), where higher values indicate greater contrast between the compared lizard signal region and the background.

2.5 Statistical analysis

2.5.1 General analytical approach

Statistical analyses were performed primarily using the R programming environment (v4.3.1) [285] and specific Python libraries detailed above. The R packages used were lme4 [286], lmerTest [287], emmeans [288], survival [289], coxme [290], brms [291, 292], pavo [275], and rptR [293].

Initial statistical models generally incorporated species identity, sex, and sampling location as fixed effects, along with their relevant interactions. Scaled SVL was included as a covariate to control body size effects. Additional potential covariates, such as sampling year, testing order, testing time, other morphological indices (SMI, limb ratios), or size-corrected residual morphometrics, were assessed via Likelihood Ratio Tests (LRT, $p < 0.05$) comparing nested models and retained only if they significantly improved model fit. A consistent model simplification approach was applied, first systematically removing non-significant interaction terms ($p \geq 0.05$) based on ANOVA comparisons, followed by removing non-significant covariates ($p \geq 0.05$) based on LRTs.

Thorough diagnostics were performed for all final models to ensure model assumptions were adequately met. These included checks for linearity, normality, and homogeneity of variance using residual plots and appropriate tests, including the Shapiro-Wilk test and Levene's test where applicable. For Generalised Linear Models (GLMs), goodness-of-fit was assessed and overdispersion was checked using Cameron and Trivedi's dispersion test or by comparing residual deviance to degrees of freedom. Transformations, including Box-Cox transformations, were applied to response variables when necessary. Multicollinearity among predictors was assessed using Variance Inflation Factors (VIFs). Potential statistical outliers or influential data points were identified using model diagnostics, including standardised residuals, leverage values, Cook's distance, and inspection of residual plots. Observations classified as outliers were removed before final model fitting. Post-hoc pairwise comparisons for significant effects or interactions were conducted using estimated marginal means via the emmeans package, with p-values adjusted using the Tukey method [288]. The significance level (α) was set at 0.05 for all tests.

2.5.2 Exploratory behaviour and neophilia/neophobia analysis

LMs were used to analyse continuous movement-related variables measured in the open field tests, including number of moving segments, distance moved, movement duration, angular velocity, and the neophobia log-ratios. Assumptions were assessed using the Shapiro-Wilk test, Levene's test, and visual inspection of diagnostic plots. Where assumptions were violated, Box-Cox transformations were applied, with λ denoting the power-transformation parameter estimated by maximum likelihood [294]. Angular velocity measurements were transformed across all trials (λ = 0.2), while other variables were transformed only where distributional assumptions were violated: distance moved (λ = 0.6 to 0.7), movement duration (λ = 0.9 to 1.2), and number of moving segments (λ = 1.2).

Negative Binomial GLMs were used to analyse contact frequency with the novel object, accounting for the discrete, non-negative nature of count data and potential overdispersion. Contact latency was analysed as time-to-event data because some individuals did not contact the object within the trial duration, producing right-censored observations. Parametric Accelerated Failure Time (AFT) models were used because they model predictor effects directly on the time to event rather than on the hazard of event occurrence [295]. The best-fitting distribution, such as Weibull, lognormal, or log-logistic, was selected based on the lowest Akaike Information Criterion (AIC) value, and effects were interpreted using acceleration factors.

2.5.3 Repeatability of behavioural traits

Adjusted repeatability (R) of movement-related variables, including number of moving segments, distance moved, movement duration, and angular velocity, was estimated across the three trials. Adjusted repeatability quantifies the proportion of the remaining phenotypic variance, after these adjustments, that is attributable to consistent among-individual differences. Trait values were first adjusted for trial, sex, and location, and repeatability was then calculated as the one-way intraclass correlation coefficient of the residuals, with individual lizard identity as the grouping factor.

Confidence intervals (95%) were obtained by cluster bootstrap, resampling individuals with replacement over 1000 iterations so that the resampling unit matched the unit of replication.

Repeatability was considered statistically significant if the 95% confidence interval did not include zero. These analyses were conducted separately for *P. melisellensis* and *P. siculus* to allow species-specific estimates and comparisons; the full estimates and intervals are reported in Table S25. Repeatability is used here only to confirm that the traits measured, namely exploration, neophobia and neophilia, and aggression, are consistent enough to shape interspecific competition between *P. siculus* and *P. melisellensis* [130]; the broader frameworks of animal personality and behavioural syndromes are not tested.

2.5.4 Aggression analysis

Latency to the first aggressive act was analysed using Cox mixed-effects proportional hazards models. This survival-analysis framework models the instantaneous risk, or hazard, of an aggressive event occurring and handles right-censored data, in this case trials in which no aggression occurred within 600 s. Whether aggression occurred and how quickly it began are distinct processes, therefore occurrence was modelled separately (Bernoulli GLMM, below). The latency model retained all trials, with non-aggressive trials right-censored rather than excluded, which uses the full dataset and avoids the selection bias that restricting the analysis to aggressive dyads would introduce. The mixed-effects structure included lizard identity to account for repeated observations of the same individuals. The proportional hazards assumption was checked using diagnostics based on Schoenfeld residuals. Model selection via LRTs assessed interactions and the contribution of size-corrected morphometric residuals.

Spatial variables from aggression trials were analysed using Linear Mixed Models (LMMs). These included the mean distance of the focal lizard from the centre of the arena and the average distance maintained between interacting lizards. Models included a random intercept for the interaction pair, and morphometric contributions were tested via LRTs.

A two-part Bayesian modelling strategy addressed aggression occurrence and type/intensity. These models included a lizard-year identifier as a random intercept and employed default weakly informative priors, defined as regularising priors that provide minimal prior information while improving model stability. Convergence was assessed using standard diagnostics: R-hat < 1.01, visual inspection of trace plots, monitoring for divergent transitions, and checking effective sample sizes. Models were compared using Leave-One-Out Information Criterion (LOOIC) [296]. Part one modelled the presence or absence of any

aggression using a Bernoulli Generalised Linear Mixed Model (GLMM) with logit link. Part two, conditional on aggression occurring, used a multivariate Negative Binomial GLMM to simultaneously model the counts of displays, chases/lunges, and bites, accounting for potential overdispersion in these counts.

2.5.5 Field anti-predator behaviour analysis

FID and FD were analysed using Linear Models (LMs). Assumptions of normality and homoscedasticity were verified via diagnostic plots. Where necessary, data were log-transformed to satisfy these assumptions.

HD was analysed using a two-part hurdle model to account for the large number of non-hiding individuals. The decision to hide was modelled using a Binomial Generalised Linear Model with logit link as a binary response (hide vs. no hide). For individuals that did hide, the duration of hiding was analysed using a Cox proportional hazards model, which appropriately handles right-censored observations, in this case animals not emerging within the 300-second observation window.

2.5.6 Colouration analysis

JND values, including chromatic contrast (dS) and luminance contrast (dL), comparing lizard body regions to reflectance-based habitat background components served as response variables in LMMs examining factors influencing visibility to predators. A two-step model selection process based on AIC and Bayesian Information Criterion (BIC) comparison was used. First, candidate models tested whether predictors representing distinct colour regions or combined predictors best explained variation, along with species, sex, and location covariates. Second, based on the best contrast structure, habitat background components, tested individually or combined, were incorporated. Final models were evaluated using ANOVAs.

To examine variation in a colour trait potentially involved in intraspecific signalling, JND values for blue UV-reflective flank spots against the surrounding brown flank background were analysed using LMs. These analyses tested whether blue spot conspicuousness varied between species, sexes, or locations.

FID, measured in the field prior to capture, was first compared between species using a Welch's t-test, then analysed within each species using LMs with predictors including sex, location, and JND metrics selected from the visibility analysis based on model selection or effect sizes.

2.5.7 Pattern analysis

Statistical analysis of pattern data corresponded to the two mentioned approaches. For the unsupervised analysis of overall pattern variation using deep features from the ResNet50 CNN, Python libraries were used. Principal Component Analysis (PCA) was used for visualisation and analysis by identifying orthogonal axes of maximum variance in the feature space.

Random Forest classification assessed how well these features could discriminate between biological groups, including species, sex, location, and their combinations. This method builds an ensemble of many individual decision trees, each trained on different data subsets, and aggregates their predictions by majority vote for classification. Performance was evaluated using balanced accuracy from stratified 5-fold cross-validation to estimate generalisation ability on unseen data while accounting for group size imbalances. Permutational multivariate tests (PERMANOVA, PERMDISP; using Euclidean distances and 999 permutations) assessed significant differences in group centroids and dispersion in the feature space.

Gradient-weighted Class Activation Mapping (Grad-CAM) was used to inspect the CNN's feature extraction process. By analysing the gradient signals flowing back into the CNN's final convolutional layers, Grad-CAM generates heatmaps that identify the specific pixels or regions in the input image that were most influential in determining the extracted features. Overlaying these heatmaps on the lizard images helped interpret which pattern elements the model used.

For the camouflage score analysis, the composite camouflage score was analysed using an LMM with background image category, species, sex, location, and interactions as fixed effects, plus individual ID as a random intercept. Model validation procedures, including

residual diagnostics and assessment of normality, were performed, and post-hoc tests for significant effects used estimated marginal means with Tukey adjustment.

3. Results

Detailed statistical outputs for all analyses — full model coefficients, complete ANOVA tables and post-hoc comparisons — are presented in the Supplementary Material (Tables S1–S26).

3.1 Exploratory behaviour and neophilia/neophobia

I examined four aspects of lizard behaviour in *Podarcis melisellensis* (PM) and *Podarcis siculus* (PS): 1) exploration in a novel environment, 2) activity in a familiar environment, 3) neophilia during exposure to a novel object, and 4) neophobia as the change in movement variables (log-ratios) between the activity and neophilia trials. Species, location, sex, and morphology affected different variables across these analyses.

3.1.1 Exploration

In the exploration trial (Figure 2), species differences were detected for several movement variables. Compared with PM, PS made fewer moving segments ($p < 0.001$), moved greater distances ($p < 0.001$), and showed higher angular velocity ($p < 0.001$). The species effect on movement duration was not significant ($p = 0.053$) (Table S1).

Location affected the number of moving segments ($p = 0.019$), movement duration ($p = 0.003$), and angular velocity ($p = 0.006$). Post-hoc tests showed that Pag lizards had more moving segments than Sinj lizards ($p = 0.046$). For movement duration, both Knin ($p < 0.001$) and Sinj ($p = 0.027$) lizards moved for longer than Pag lizards. Sinj lizards also had higher angular velocity than Knin lizards ($p = 0.020$). Body size (Snout-Vent Length, SVL) was a positive (higher values of variables with higher values of SVL) predictor of distance moved ($p = 0.012$), movement duration ($p = 0.003$), and angular velocity ($p = 0.019$). Sex did not affect any of the measured variables during exploration. These movement-related traits are shown in Figure 2 (Table S2).

3.1.2 Activity

In the activity trial (Figure 2), species effects remained for the number of moving segments (PM higher; $p < 0.001$) and angular velocity (PS higher; $p = 0.039$), but not for distance

moved or movement duration. The species-by-location interaction was removed as non-significant during model simplification, so the species effects were consistent across locations. Location affected the number of moving segments ($p = 0.001$), distance moved ($p = 0.048$), movement duration ($p = 0.008$), and angular velocity ($p = 0.041$). Post-hoc comparisons showed that Knin lizards moved greater distances than Pag ($p = 0.003$), Knin lizards had longer movement durations than both Pag ($p = 0.046$) and Sinj ($p = 0.002$), and Sinj lizards had higher angular velocity than Knin ($p = 0.013$). Sex was significant in this trial, with males showing higher angular velocities than females ($p = 0.016$). SVL was negatively associated with the number of moving segments ($p = 0.022$).

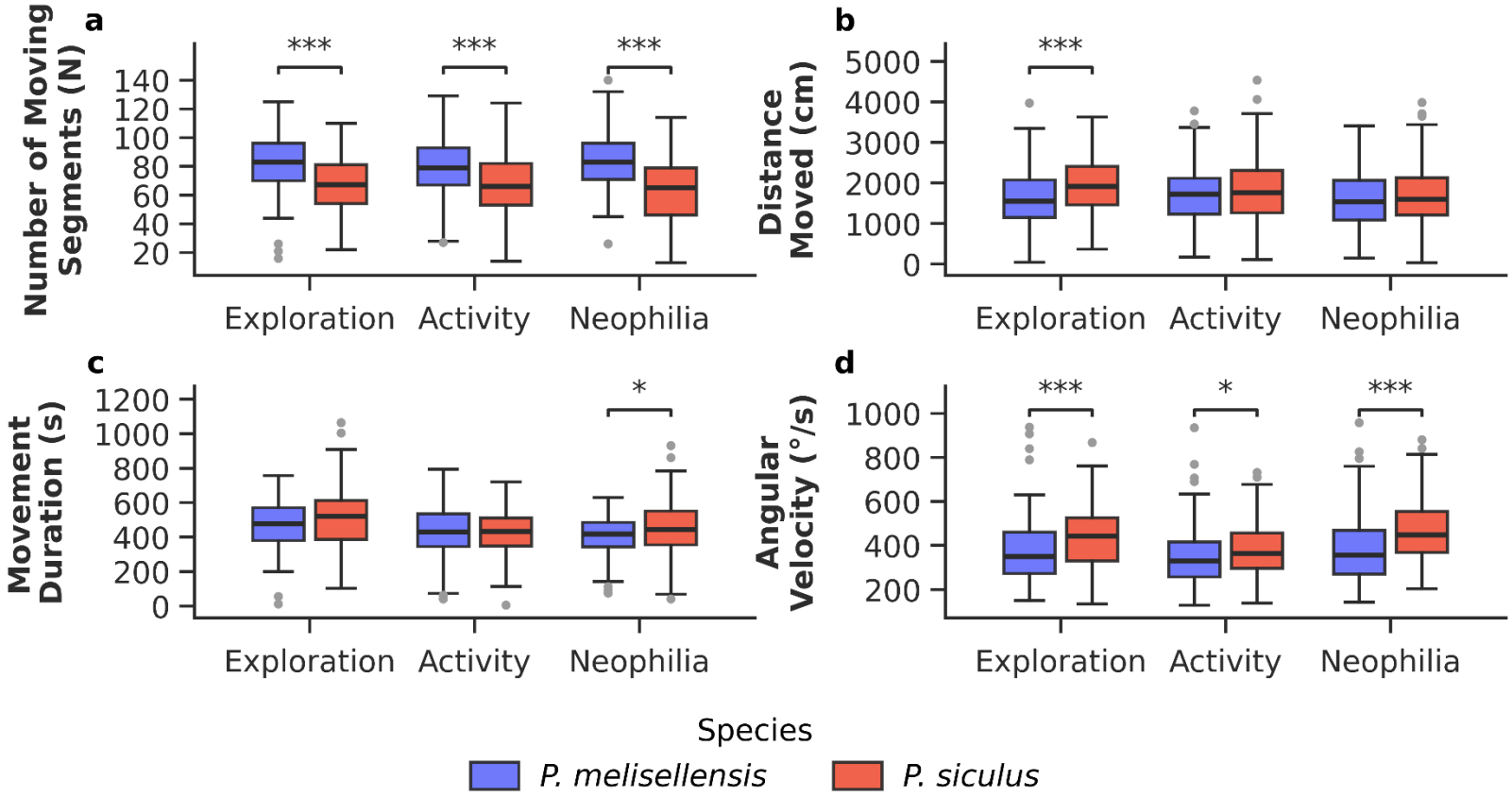

Figure 2. Comparison of movement-related traits between *Podarcis melisellensis* and *Podarcis siculus* across different trials. a) number of moving segments (N); b) distance moved (cm); c) movement duration (s); d) angular velocity (°/s). Data are presented as the median (central line), interquartile range (IQR, box), range within 1.5 times the IQR (whiskers), and outliers (individual points beyond the whiskers). * $p < 0.05$, *** $p < 0.001$.

3.1.3 Neophilia

In the neophilia trial (Figure 2), species was significant for the number of moving segments (PM higher; $p < 0.001$), movement duration (PS longer; $p = 0.010$), and angular velocity (PS higher; $p < 0.001$). Location affected the number of moving segments ($p < 0.001$) and angular velocity ($p = 0.002$): Sinj lizards had higher angular velocity than Knin ($p = 0.012$) and Pag ($p = 0.035$), while Pag lizards had more moving segments than Sinj ($p = 0.002$). Sex was significant for angular velocity, with males showing higher values than females ($p = 0.002$). Morphological effects were specific to this trial: SVL negatively affected the number of moving segments ($p = 0.012$), and Scaled Mass Index (SMI) negatively affected angular velocity ($p = 0.029$) (Table S1).

In the AFT model (log-logistic distribution; Table S4), species affected interactions with the novel object (Figure 3): PS had higher contact frequency ($p = 0.001$) and shorter contact latency ($p = 0.048$) than PM. Location did not affect contact frequency or contact latency. Sex affected both variables: males had higher contact frequency ($p = 0.004$) and shorter contact latency ($p = 0.048$) than females (Table S5).

3.1.4 Neophobia

Neophobia was assessed by comparing the activity and neophilia trials (Figure 4). The log-ratio of movement duration showed significant effects of species ($p = 0.008$), location ($p = 0.003$), and a species-by-location interaction ($p = 0.002$). Post-hoc tests indicated that PM from Knin had a lower log-ratio (greater reduction in duration) than PS from Knin ($p = 0.029$), PM from Pag ($p = 0.018$), PM from Sinj ($p = 0.029$), and PS from Sinj ($p = 0.018$). This pattern indicates a stronger neophobic response in PM from Knin. The log-ratio of angular velocity was affected only by species ($p = 0.012$), with PS maintaining relatively higher velocity. The fixed effects were not significantly related to the log-ratios for the number of moving segments or distance moved (Table S3).

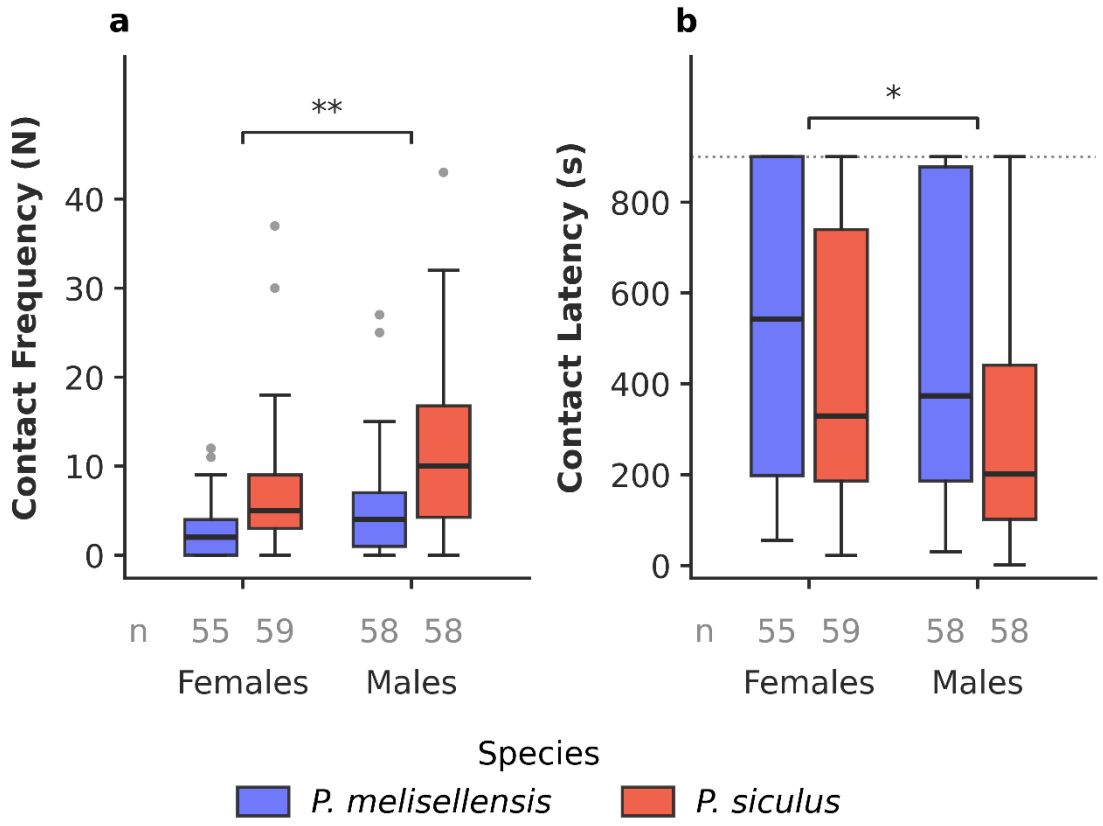

Figure 3. a) Contact frequency (N) and b) contact latency (s) to a novel object in *Podarcis melisellensis* and *Podarcis siculus*, shown separately for females and males. Data are presented as the median (central line), interquartile range (IQR, box), range within 1.5 times the IQR (whiskers), and outliers (individual points beyond the whiskers). The dotted line in panel b marks the 900 s trial limit, where individuals that never contacted the object are right-censored. * $p < 0.05$ ** $p < 0.01$.

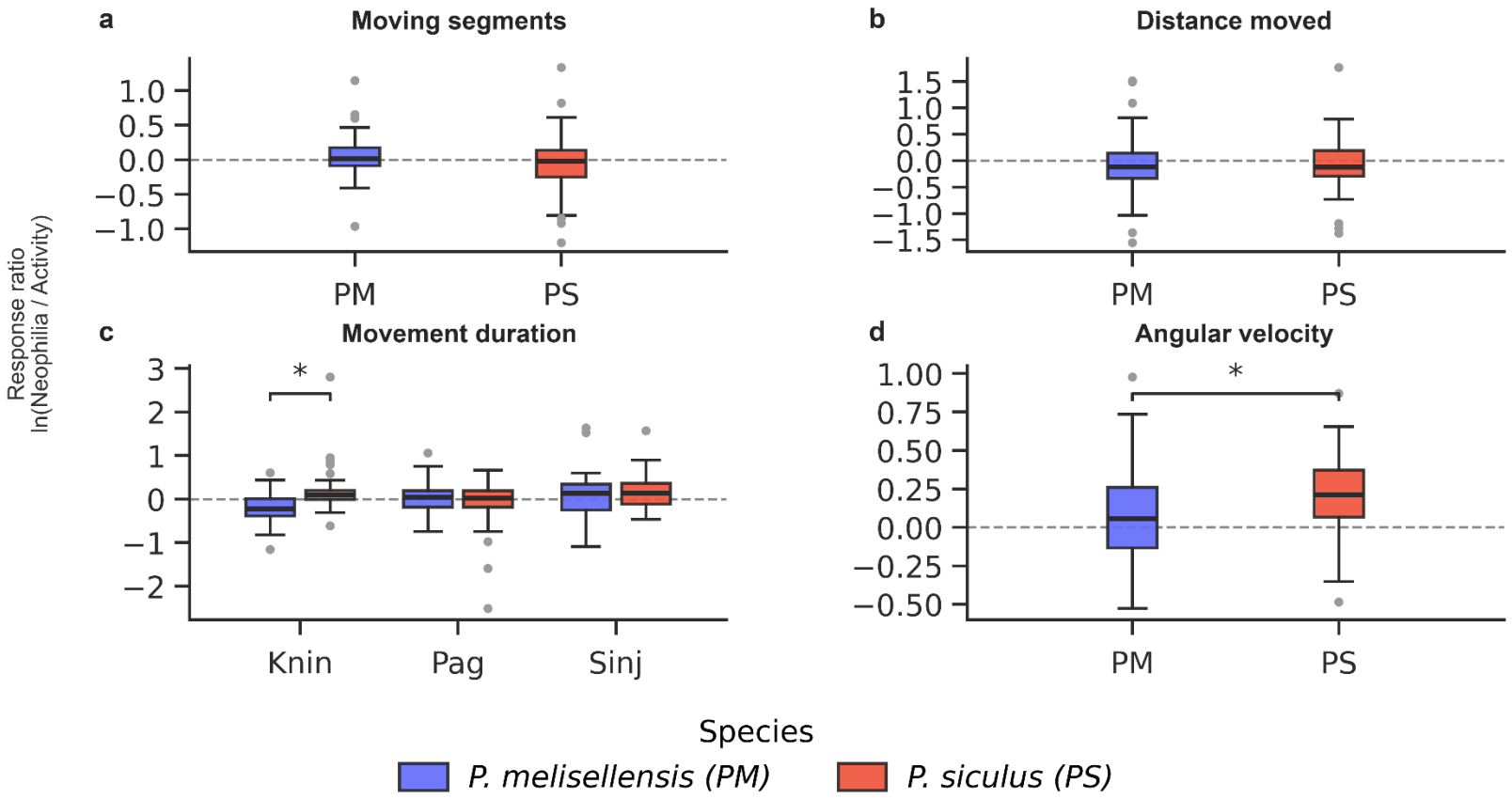

Figure 4. Comparison of neophobia between *Podarcis melisellensis* (PM) and *Podarcis siculus* (PS) from three locations, expressed as log ratios of movement-related trait values from neophilia and activity trials; a) number of moving segments; b) distance moved; c) movement duration; d) angular velocity. Movement duration is shown as a pairwise comparison of species across locations because it was the only variable with a significant species-by-location interaction. Data are presented as the median (central line), interquartile range (IQR, box), range within 1.5 times the IQR (whiskers), and outliers (individual points beyond the whiskers). * $p < 0.05$.

3.1.5 Repeatability and covariates

Adjusted repeatability analyses (Figure 5) revealed significant individual consistency in movement patterns for both species after adjusting for trial, sex, and location (Table S25). For PM, all four movement variables were significantly repeatable, with estimates ranging from R = 0.36 (movement duration) to R = 0.63 (angular velocity) and 95% confidence intervals excluding zero throughout. PS was likewise significantly repeatable across all variables, with estimates from R = 0.35 (number of moving segments) to R = 0.55 (angular velocity). The confidence intervals of the two species overlapped for every variable, so the data give no evidence of a species difference in repeatability.

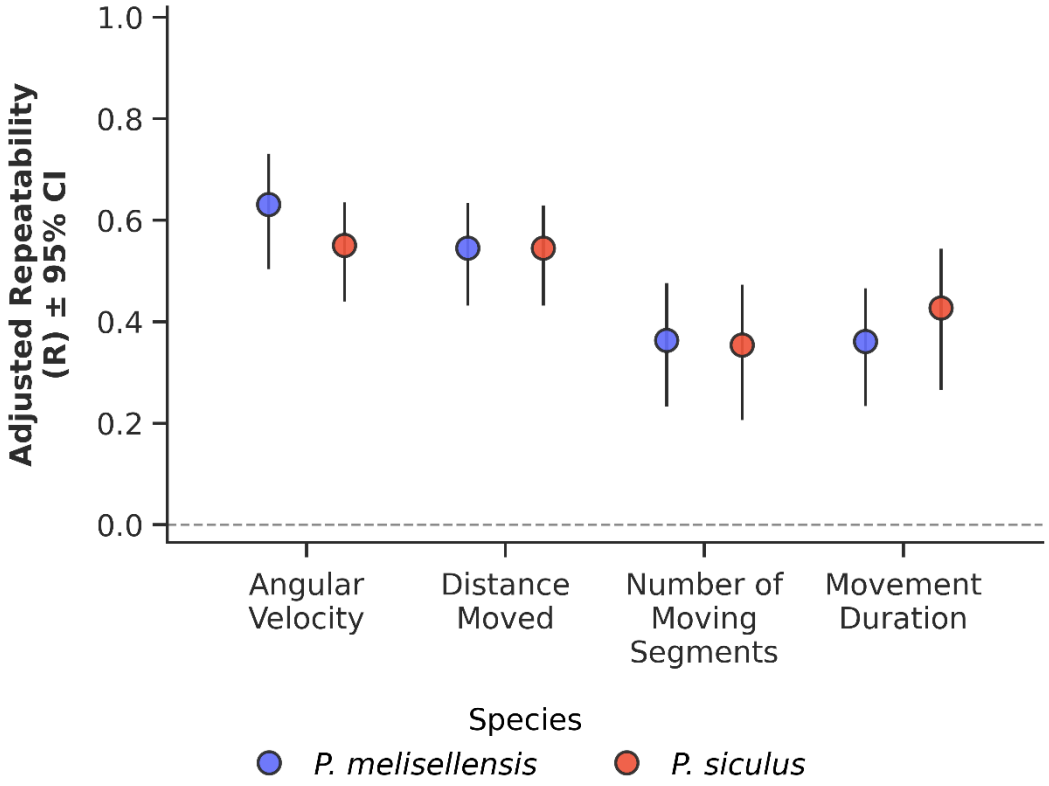

Figure 5. Adjusted repeatability (R) with 95% confidence intervals for four movement-related traits – angular velocity, distance moved, number of moving segments, and movement duration – estimated across the three trials (exploration, activity, neophilia) for *Podarcis melisellensis* and *Podarcis siculus*. R is the one-way intraclass correlation of residuals after adjusting for trial, sex, and location; whiskers denote cluster-bootstrap 95% confidence intervals from 1000 resamples over individuals. Confidence intervals that exclude zero indicate significant individual consistency. The plotted values are those reported in Table S25.

In addition to SVL, I assessed the potential contribution of other morphological indices—specifically Scaled Mass Index (SMI), interlimb ratio, and hindlimb-to-forelimb ratio—as covariates in the models. These indices were retained only if their inclusion led to a significant improvement in model fit, determined via Likelihood Ratio Tests ($p < 0.05$). The analyses revealed that neither the interlimb ratio nor the hindlimb-to-forelimb ratio met this criterion for significance across any of the behavioural variables or trials examined; hence they were excluded from the final model. SMI was found to be significant in only one instance: in the neophilia trial, SMI significantly negatively influenced angular velocity for both species ($p = 0.029$). Apart from this specific effect, SMI did not significantly explain variation in other behaviours or trials.

Year of sampling did not significantly influence the measured behavioural variables across any trials. Time of testing showed only one specific significant effect: it influenced angular velocity in the exploration trial ($p = 0.030$). Time of testing did not significantly affect the other behavioural variables measured within this trial (distance moved, movement duration, number of moving segments), nor did it significantly influence any measured variables in the subsequent trials.

Across all trials, PM exhibited a higher number of moving segments, whereas PS consistently displayed greater angular velocity. Two variables were trial-dependent: PS moved greater distances only in the exploration trial and exhibited longer movement durations only in the neophilia trial. Sex effects were absent in exploration but emerged during activity and neophilia trials. SVL was positively associated with movement (distance moved, movement duration, and angular velocity) in the exploration (novel-environment) trial, but negatively associated with the number of moving segments in the activity (familiar) and neophilia trials. Location effects differed by variable, with Sinj lizards often showing higher angular velocities than lizards from other locations, depending on the trial. PM showed higher neophobia, particularly lizards from Knin, with shorter movement durations. Both species showed high repeatability across variables.

3.2 Aggression

Aggression was significantly more frequent and intense in within-species encounters compared to between-species encounters. Females exhibited fewer aggressive behaviours

(almost exclusively displays) than males, who engaged in three escalating categories of aggression: displays (the least intense), chases/lunges, and bites (the most intense). PS showed a shorter latency to aggression compared to PM (Cox model, HR ≈7.57, $p = 0.013$), and males were faster to aggress than females (HR ≈8.20, $p < 0.001$; Figures 8–9). Body morphology (size-corrected morphometric residuals), location, and year of study did not influence aggressive behaviour.

I investigated multiple facets of aggressive interactions: the overall occurrence of aggression, the types and intensity of aggressive acts, the latency to the first aggressive act, and spatial positioning (distance from centre and inter-individual distance).

An initial overview of the data showed baseline aggression patterns (Figure 6). Aggression was observed in a minority of trials, but its prevalence varied greatly depending on the encounter type. Males were substantially more likely to be aggressive than females. This sex difference was particularly pronounced in PS, where 25.4% of males were aggressive in between-species encounters and 60.7% in within-species encounters, compared to 7.0% and 5.2% for females, respectively. Aggression was very rare in PM between-species encounters (1.6–1.8% across sexes) but increased notably for males in within-species encounters (26.6%).

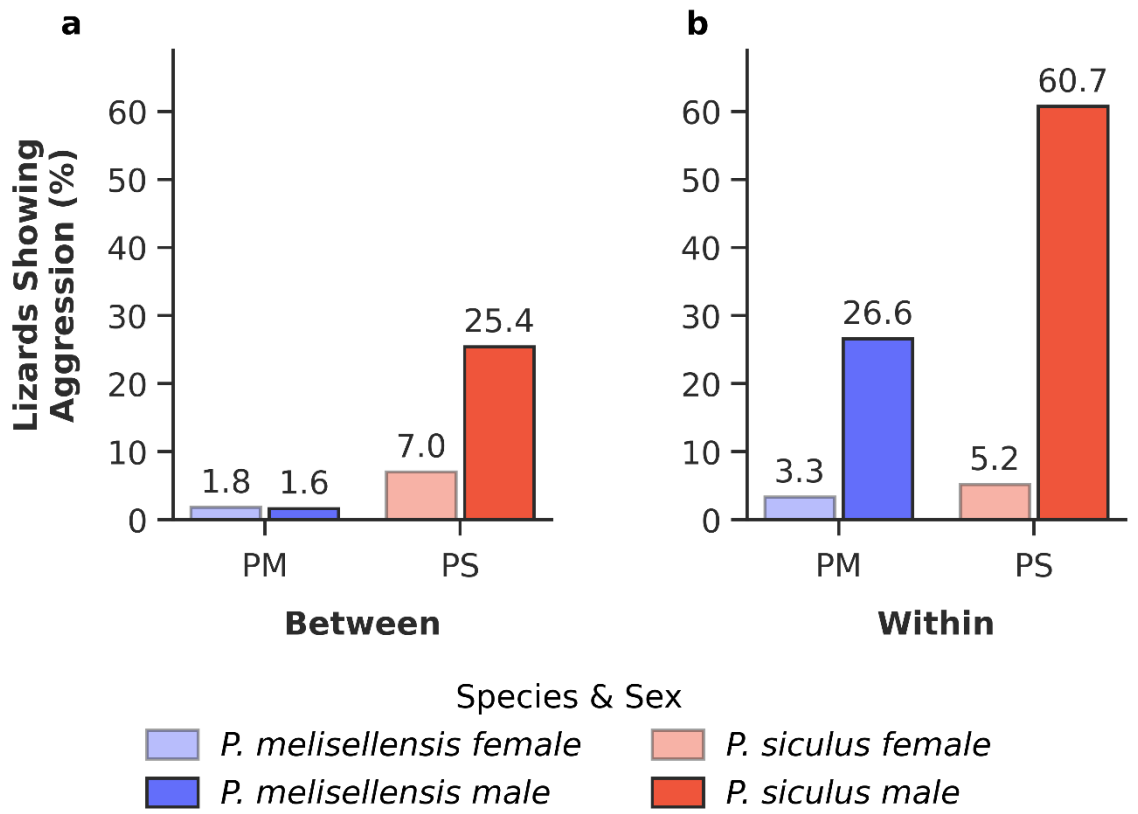

Figure 6. Percentage of lizards that showed any sign of aggression during dyadic encounters in *Podarcis melisellensis* (PM) and *Podarcis siculus* (PS), shown separately for a) between-species (heterospecific) and b) within-species (conspecific) encounters. Bars are split by sex (lighter fill = females, saturated fill = males) and labelled with the corresponding percentage. Percentages are calculated per unique individual within each encounter type: an individual counts as having shown aggression if its aggression score exceeded zero in that encounter type.

A Bayesian Bernoulli GLMM confirmed that aggression was significantly more likely during encounters between members of the same species (within-species) compared to encounters between different species (Median log-odds difference ≈1.38, 95% CI: [0.77, 2.01]). The sex of the lizard was also a major factor, with males being significantly more likely to show aggression than females (Median log-odds difference F−M ≈−2.12, CI: [−2.94, −1.39]). PS was somewhat more prone to aggression overall than PM, although the credible interval approached zero (Median log-odds difference ≈−0.96, CI: [−1.83, −0.05]). Geographic location and morphology did not significantly predict whether aggression would occur.

Furthermore, the type of aggression differed (Figure 7): aggressive acts by females of both species, and by males in between-species encounters, were almost exclusively displays. In contrast, males engaging in within-species aggression utilised a combination of displays, chases/lunges, and bites. Bites constituted a larger proportion of acts for PS males (48.7%) than for PM males (30.6%) among those showing aggression. Displays were the most common form: they occurred in just 1.8–3.3% of PM females, 1.6% of PM males in between-species trials, and 5.2–5.3% of PS females, but rose to 23.8% of PS males in between-species trials and 44.6% in within-species trials. Escalation to chases or lunges occurred almost exclusively in male within-species encounters, reaching 4.7% of PM males and 32.1% of PS males, with a single chase by a PS female in a between-species trial. Biting followed the same pattern, being absent in females and recorded in a single between-species contest (one PS male), but reaching 7.8% of PM males and as many as 37.5% of PS males during within-species encounters.

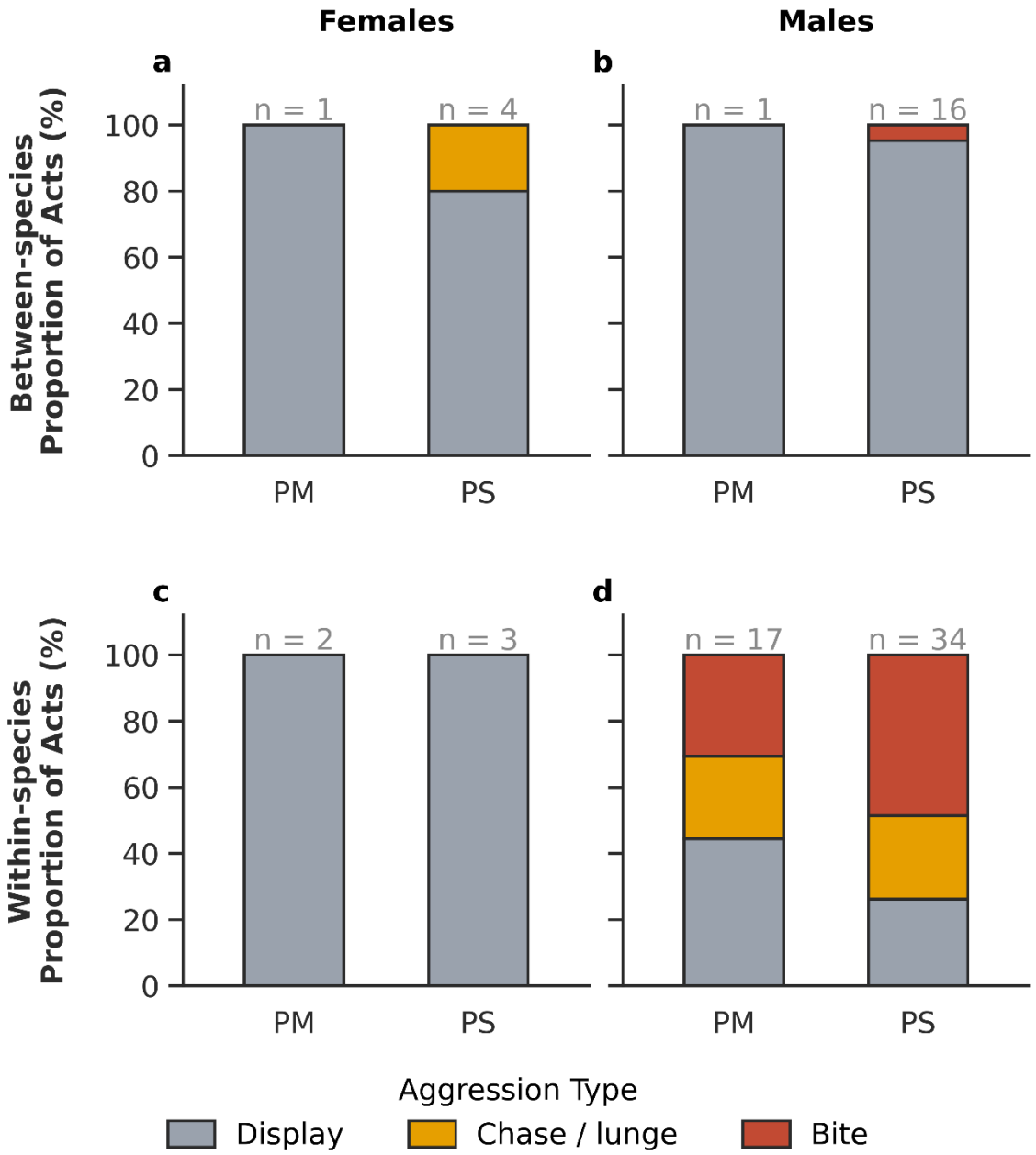

Figure 7. Composition of aggressive acts performed by lizards that showed aggression in *Podarcis melisellensis* (PM) and *Podarcis siculus* (PS), expressed as the relative proportion (%) of displays, chases/lunges, and bites. Panels show between-species (heterospecific) encounters for a) females and b) males, and within-species (conspecific) encounters for c) females and d) males. Proportions are calculated across the aggressive acts recorded for the unique individuals that showed aggression in that encounter type; individuals that showed no aggression do not contribute. The number of individuals behind each bar is given above the bar.

Among the subset of aggressive individuals (N=76), a Multivariate Negative Binomial GLMM showed that none of the tested factors significantly predicted the number of displays. However, for more intense acts, encounter type mattered. Significantly fewer lunges/chases occurred during between-species encounters compared to within-species encounters (CI: [−18.45, −2.75]). Similarly, significantly fewer bites occurred in between-species encounters (CI: [−20.40, −3.73]). Among those individuals that showed aggression, males performed significantly higher numbers of both lunges/chases (CI: [0.34, 32.45]) and bites (CI: [3.47, 37.55]) than females.

Latency to the first aggressive act (Figure 8) was analysed using Cox mixed-effects models (Tables S6, S7). Males initiated aggression significantly faster than females, having approximately 8.2 times the hazard rate (HR ≈8.20, $p < 0.001$). Aggression also occurred significantly faster during within-species encounters compared to between-species encounters (HR ≈10.75, $p = 0.002$). PS displayed significantly shorter latencies than PM, having about 7.6 times the hazard rate (HR ≈7.57, $p = 0.013$). Although the raw median latency appears higher for PS because non-aggressive trials were right-censored at 600 s, the Cox model and the Kaplan–Meier curves (Figure 9) show that PS actually initiated aggression sooner than PM. The encounter-type-by-species interaction was not significant ($p = 0.052$). Exploratory post-hoc tests confirmed that PS was significantly faster than PM in both between-species ($p = 0.007$) and within-species encounters ($p = 0.027$) (Tables S6 and S7).

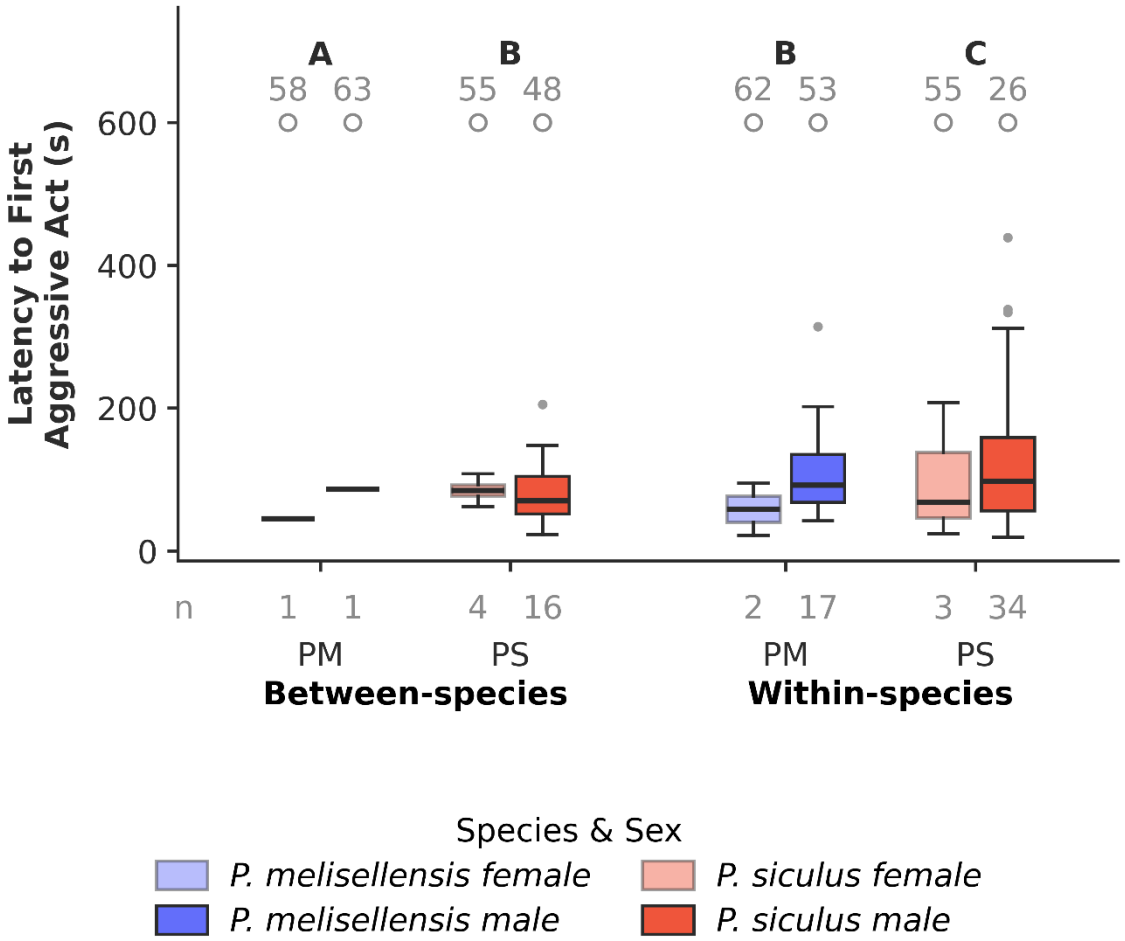

Figure 8. Latency (s) to the first aggressive act in *Podarcis melisellensis* (PM) and *Podarcis siculus* (PS), by encounter type (between-species = heterospecific encounter; within-species = conspecific encounter), with each species split by sex (lighter fill = females, saturated fill = males). Data are presented as the median (central line), interquartile range (IQR, box), range within 1.5 times the IQR (whiskers), and outliers (individual points beyond the whiskers). Boxes summarise only those trials in which aggression occurred, and n below each box gives how many trials that is; three of the eight boxes rest on one or two trials, so their position should not be read as a species difference. Trials with no aggressive act within the 600 s observation period are right-censored and are shown as open circles at the censoring limit, with the number of censored trials given in grey above each group. Capital letters above each species × encounter-type group summarise the Tukey-adjusted post-hoc contrasts from the Cox mixed-effects model (Table S7): groups that share no letter differ significantly ($p < 0.05$). The model is fitted to all trials, censored ones included, and treats sex as an additive term; males initiated aggression faster than females in every group (HR ≈ 8.20, $p < 0.001$; Table S6).

The Kaplan–Meier curves (Figure 9) show the temporal pattern of aggression. The within-species curve rises earlier and more steeply than the between-species curve, and PS reaches higher cumulative probabilities sooner than PM. This is consistent with the Cox model results showing shorter latency in within-species encounters and in PS.

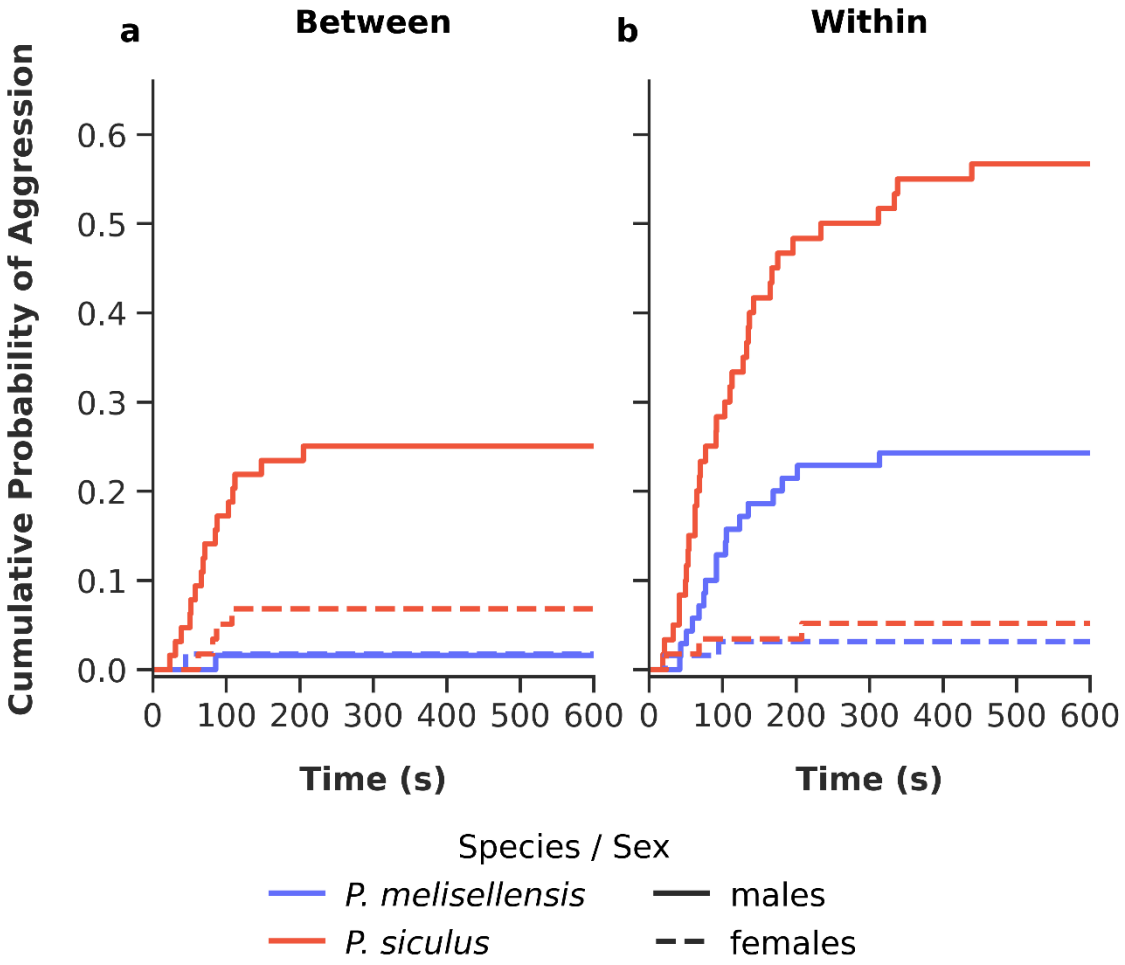

Figure 9. Cumulative probability of aggression over time during dyadic encounters (Kaplan–Meier estimator) in *Podarcis melisellensis* and *Podarcis siculus*, shown separately for a) between-species and b) within-species encounters, with males as solid lines and females as dashed lines. Steeper curves indicate faster onset of aggression. All trials contribute, with trials showing no aggression within 600 s treated as right censored.

Regarding spatial behaviour, I first analysed the average distance lizards maintained from the centre of the arena using LMMs (Figure 10). Encounter type significantly affected this distance ($p < 0.001$), and there was a significant interaction between focal species and encounter type ($p < 0.001$). Post-hoc tests (Table S9) showed that both species stayed a similar distance from the centre during between-species encounters ($p = 0.974$). However, PM stayed significantly closer to the centre during within-species encounters compared both to their between-species positioning ($p = 0.005$) and to PS during within-species encounters ($p < 0.001$). In contrast, PS showed no significant change in distance from the centre between encounter types ($p = 0.259$) (Tables S8 and S9). Sex was included in this model and had no significant effect on the distance maintained from the arena centre (Table S8).

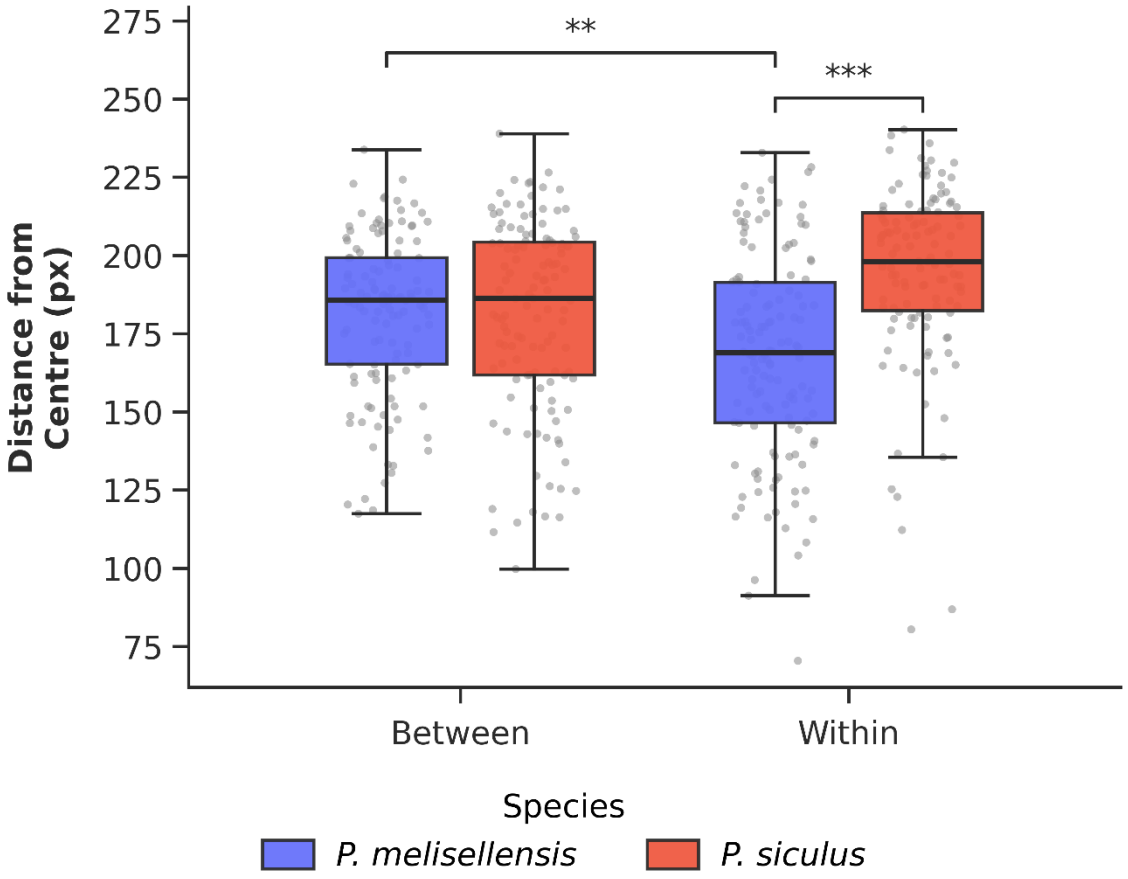

Figure 10. Distance from the centre of the arena (pixel) maintained by lizards during dyadic encounters in *Podarcis melisellensis* and *Podarcis siculus*, compared across between-species (Between) and within-species (Within) encounter types. Data are presented as the median (central line), interquartile range (IQR, box), and range within 1.5 times the IQR (whiskers); individual data points are shown with horizontal jitter. ** $p < 0.01$, *** $p < 0.001$.

I also analysed the average distance maintained between the two interacting lizards using LMMs (Figure 11; Table S10). This distance was significantly influenced by encounter type ($p = 0.039$). Post-hoc tests (Table S11) revealed that, compared to within-species encounters involving PM, lizards maintained significantly greater distances during between-species encounters ($p = 0.027$), and within-species PS encounters ($p = 0.022$). The distance during between-species encounters was not significantly different from that during within-species PS encounters ($p = 0.612$). Neither sex, location, nor body size (size-corrected morphometric residuals) significantly predicted the distance between lizards (Tables S10 and S11).

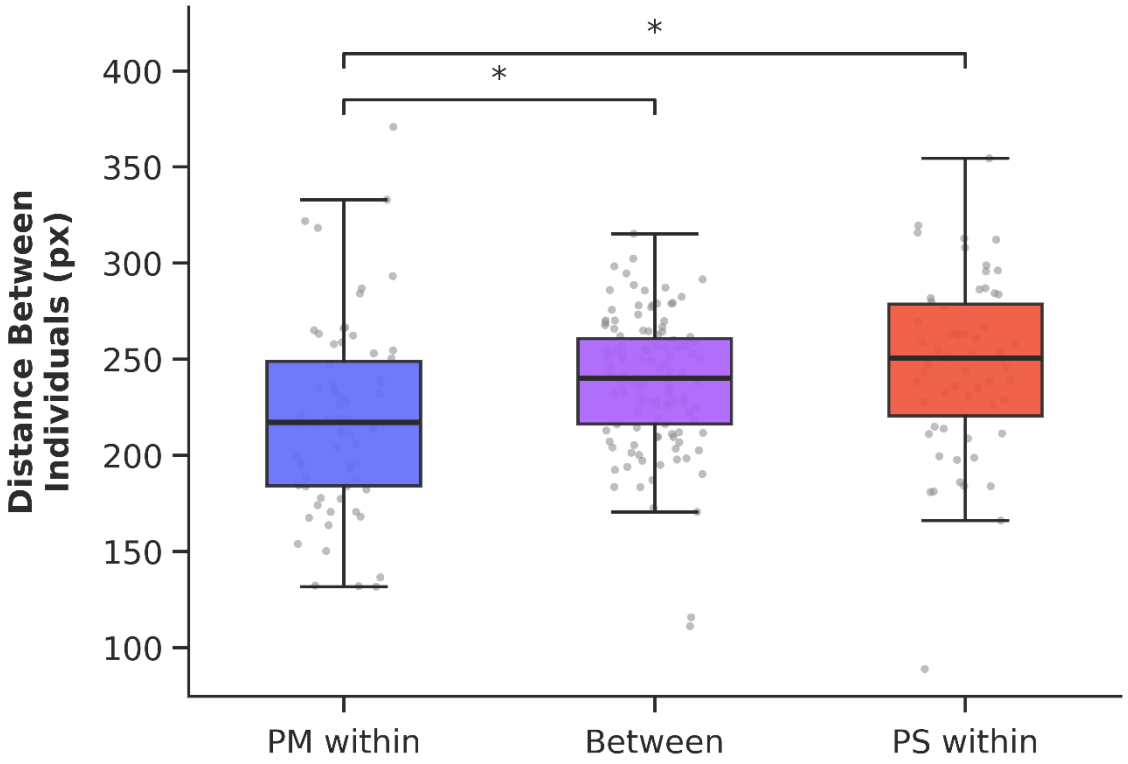

Figure 11. Average distance (pixel) maintained between the two interacting lizards during dyadic encounters in *Podarcis melisellensis* (PM) and *Podarcis siculus* (PS), compared across three dyad types: both individuals PM (PM within, blue), one individual of each species (between, purple), and both individuals PS (PS within, red). Data are presented as the median (central line), interquartile range (IQR, box), range within 1.5 times the IQR (whiskers), and individual data points shown with horizontal jitter. * $p < 0.05$.

3.3 Anti-predator behaviour and visibility

3.3.1 Flight initiation distance (FID)

PS exhibited significantly greater flight initiation distances (FID) than PM ($p < 0.001$; Figure 12). PM FID was significantly influenced by location: lizards from Pag allowed closer approach (lower FID) than those from Knin ($p = 0.009$) and Sinj ($p = 0.022$) (Table 4). For PM, habitat background components also affected FID differently depending on the predator model. In models based on snake vision, higher chromatic and luminance contrasts against leaf and grass habitat background components were associated with greater FID, whereas higher contrast against branch backgrounds was associated with shorter FID. This branch effect was significant for both chromatic contrast ($p = 0.041$) and luminance contrast ($p = 0.018$). In contrast, in models based on bird vision, higher chromatic contrast against stone and ground habitat background components decreased FID ($p = 0.038$), the corresponding luminance effect falling short of significance ($p = 0.071$), while higher luminance contrast against leaf and grass, as well as anthropogenic habitat background components, increased FID. For PS, by contrast, FID was not influenced by habitat background components, predator visual components, location, or sex (Table 5). Full ANOVA results for flight initiation distance are reported in Table 4 (*P. melisellensis*) and Table 5 (*P. siculus*) (Table S13).

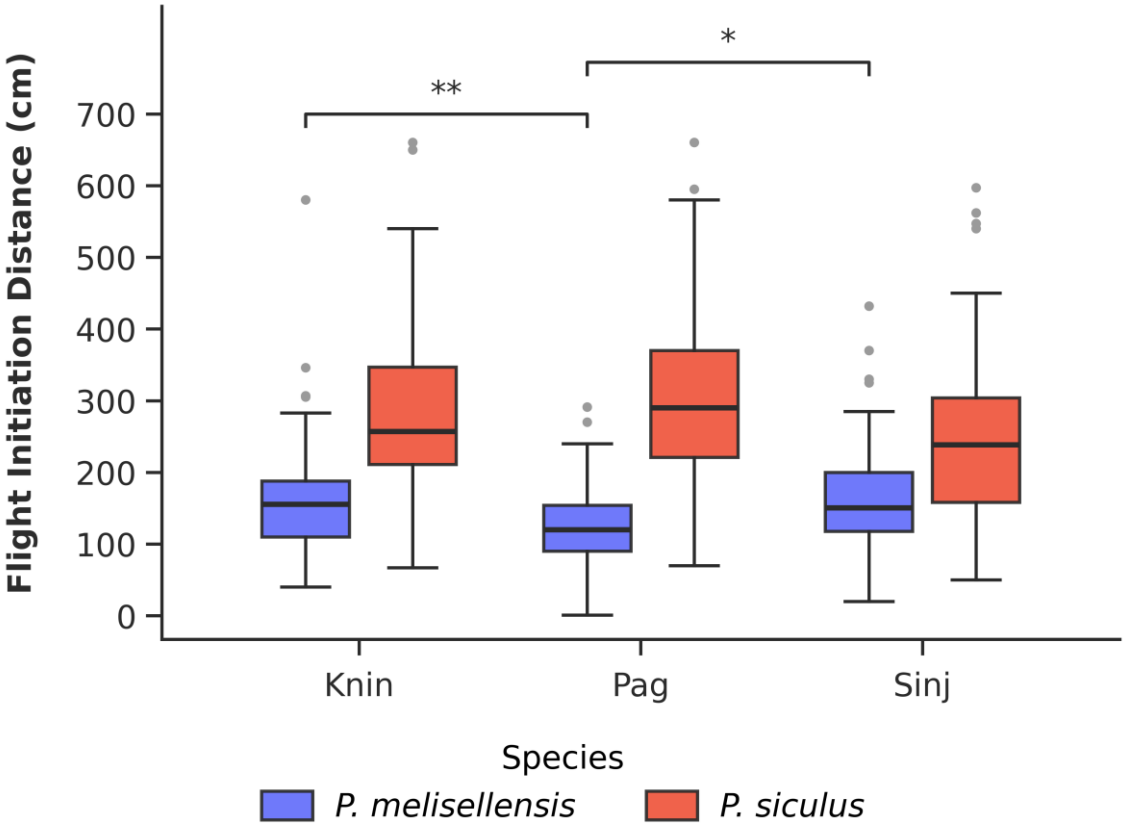

Figure 12. Flight initiation distance (FID, cm) in response to approaches in *Podarcis melisellensis* and *Podarcis siculus* at the three sampling locations. Data are presented as the median (central line), interquartile range (IQR, box), range within 1.5 times the IQR (whiskers), and outliers (individual points beyond the whiskers). * $p < 0.05$, ** $p < 0.01$.

Table 4. Summary of ANOVA results assessing the effects of sex, location, and visual contrast components (chromatic and luminance) from models based on visibility to bird and snake predators on the flight initiation distance (FID) of *P. melisellensis* (PM). Fitted on the colouration subset (N = 30). Significant effects ($p < 0.05$) are shown in bold.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Sex	1	0.8683	0.8683	4.4740	0.0605
Location	**2**	**3.1789**	**1.5894**	**8.1897**	**0.0078**
Predator					
Bird					
Chromatic contrast					
Stone x ground	**1**	**1.1127**	**1.1126**	**5.7331**	**0.0376**
Leaf x grass	1	0.0111	0.0110	0.0570	0.8161
Anthropogenic	**1**	**1.5068**	**1.5068**	**7.7640**	**0.0192**
Branch	1	0.3845	0.3844	1.9811	0.1895
Luminance contrast					
Stone x ground	1	0.7941	0.7941	4.0917	0.0706
Leaf x grass	**1**	**0.9953**	**0.9953**	**5.1284**	**0.0470**
Anthropogenic	**1**	**1.3308**	**1.3308**	**6.8571**	**0.0256**
Branch	1	0.2892	0.2891	1.4899	0.2502
Snake					
Chromatic contrast					
Stone x ground	1	0.4385	0.4385	2.2595	0.1637

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Leaf x grass	**1**	**1.7064**	**1.7064**	**8.7925**	**0.0141**
Anthropogenic	1	0.5102	0.5101	2.6287	0.1360
Branch	**1**	**1.0649**	**1.0649**	**5.4869**	**0.0411**
Luminance contrast					
Stone x ground	1	0.6515	0.6515	3.3569	0.0968
Leaf x grass	**1**	**2.0124**	**2.0124**	**10.369**	**0.0091**
Anthropogenic	1	0.0082	0.0082	0.0422	0.8413
Branch	**1**	**1.5572**	**1.5571**	**8.0233**	**0.0177**

Table 5. Summary of ANOVA results assessing the effects of sex, location, and visual contrast components (chromatic and luminance) from models based on visibility to bird and snake predators on the flight initiation distance (FID) of *P. siculus* (PS). Fitted on the colouration subset (N = 30). Significant effects ($p < 0.05$) are shown in bold.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Sex	1	0.0475	0.04754	0.0578	0.8160
Location	2	0.8807	0.44037	0.5357	0.6048
Predator					
Bird					
Chromatic contrast					
Stone x ground	1	0.1492	0.14925	0.1816	0.6813

		Df	Sum Sq	Mean Sq	F value	Pr(>F)
	Leaf x grass	1	0.1651	0.16511	0.2009	0.6659
	Anthropogenic	1	0.0146	0.01463	0.0178	0.8972
	Branch	1	1.1938	1.1938	1.4523	0.2626
	Luminance contrast					
	Stone x ground	1	0.8345	0.83453	1.0153	0.3431
	Leaf x grass	1	0.2570	0.25696	0.3126	0.5914
	Anthropogenic	1	2.0117	2.01168	2.4474	0.1564
	Branch	1	1.1581	1.1581	1.4089	0.2693
Snake						
	Chromatic contrast					
	Stone x ground	1	0.5107	0.51075	0.6214	0.4533
	Leaf x grass	1	0.6061	0.60607	0.7373	0.4155
	Anthropogenic	1	0.4038	0.40384	0.4913	0.5032
	Branch	1	0.1418	0.14184	0.1726	0.6888
	Luminance contrast					
	Stone x ground	1	0.3768	0.37682	0.4584	0.5175
	Leaf x grass	1	1.1509	1.15092	1.4002	0.2707
	Anthropogenic	1	0.6375	0.63754	0.7756	0.4042
	Branch	1	0.3582	0.35821	0.4358	0.5277

3.3.2 Flight distance (FD)

Analysis of flight distance (FD), defined as the distance lizards fled before stopping, revealed a significant main effect of species ($p < 0.001$; Figure 13). PS fled significantly greater distances than PM. While the main effect of sex was not significant ($p = 0.14$), there was a significant species-by-sex interaction ($p = 0.047$). The main effect of location was not significant ($p = 0.818$), and no other interaction reached significance (Table S14).

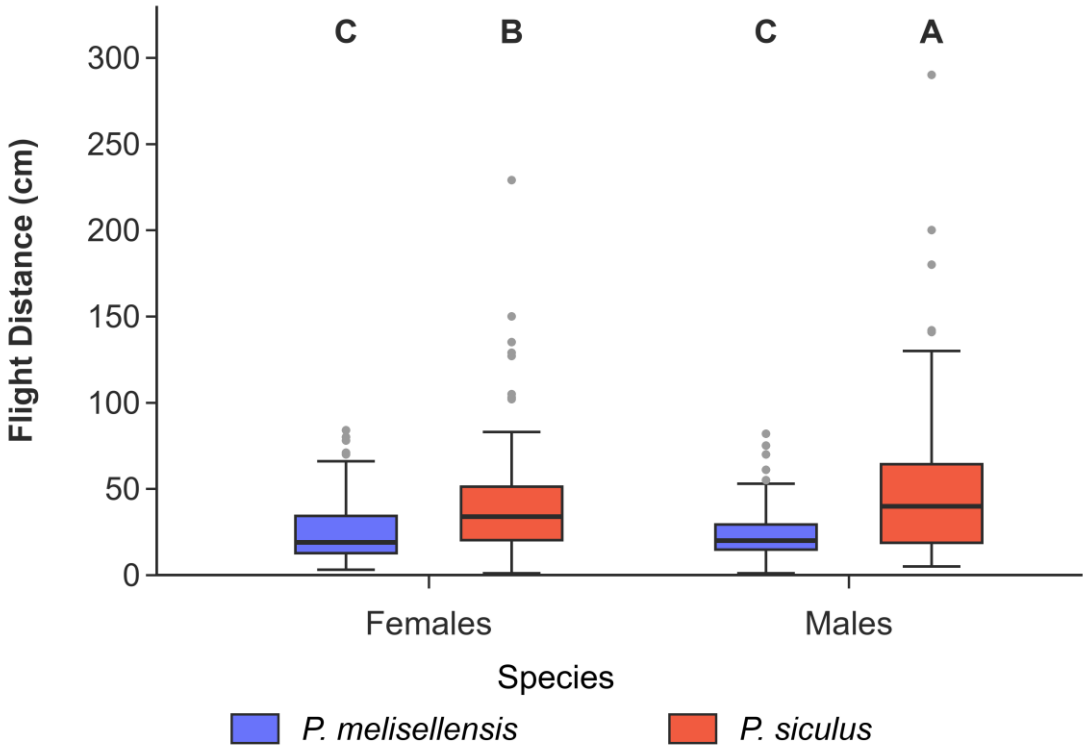

Figure 13. Flight distance (cm), defined as the distance fled before stopping in response to approach, in *Podarcis melisellensis* and *Podarcis siculus*, shown separately for females and males. Data are presented as the median (central line), interquartile range (IQR, box), range within 1.5 times the IQR (whiskers), and outliers (individual points beyond the whiskers). Capital letters summarize all six Holm-adjusted pairwise contrasts among model-adjusted species-by-sex means: groups sharing a letter do not differ significantly, whereas groups with different letters differ at $p < 0.05$. The model used all 452 observations, including the 600 cm record omitted from the plot.

3.3.3 Hiding duration (HD)

Hiding behaviour was analysed using a two-part hurdle model (Figure 14). First, the decision to hide (binary response) was modelled using logistic regression. Time of day was a significant predictor ($p = 0.008$), with lizards tested later in the day being less likely to hide. A significant three-way interaction between species, sex, and location (specifically Pag) was detected ($p = 0.037$), indicating that the propensity to hide depends on complex local demographic factors (Table S15). However, regarding the second component —the duration of hiding for those that did hide (N = 143)— the Cox proportional hazards model revealed no significant predictors. Neither species ($p = 0.88$), sex ($p = 0.43$), location (Pag $p = 0.56$, Sinj $p = 0.23$), nor time of day ($p = 0.69$) significantly influenced the time until emergence. Hiding duration itself did not differ between species, or sex, location, or time of day; once a lizard had entered refuge, how long it stayed hidden appears to be governed by factors shared across both species rather than by species identity (Table S16).

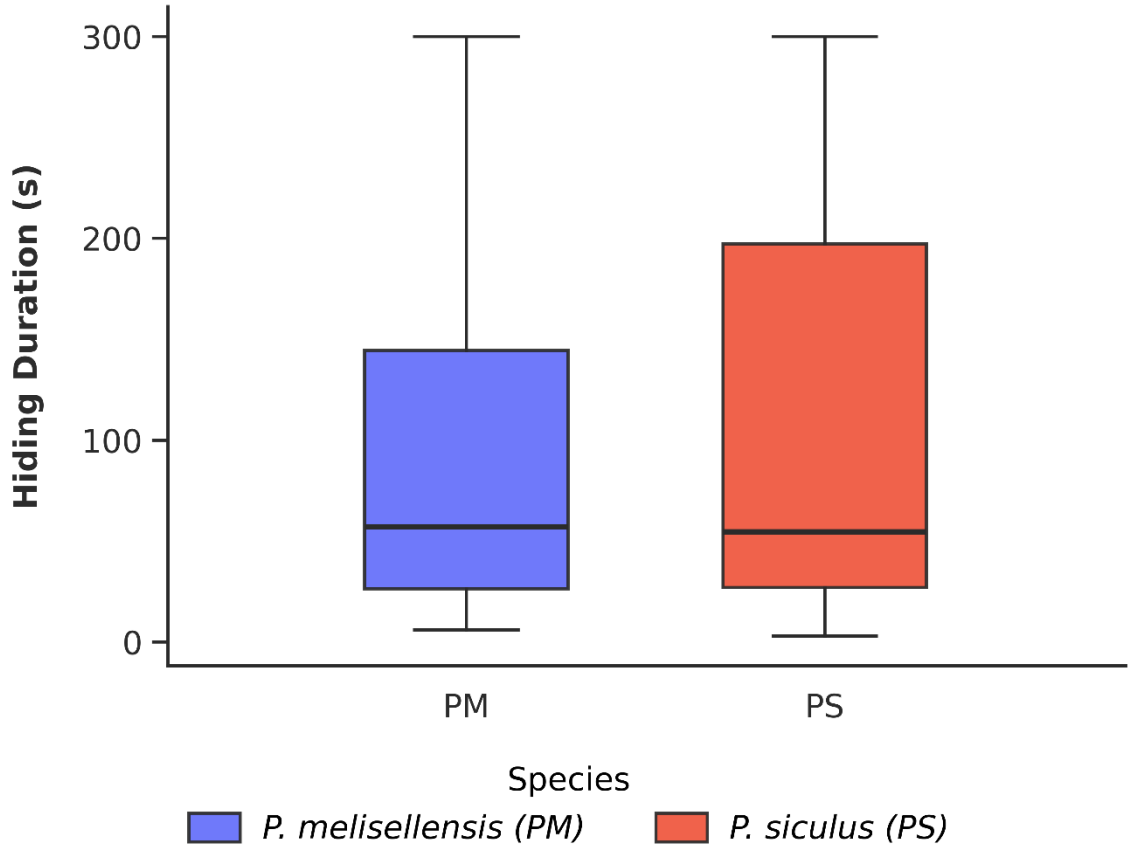

Figure 14. Hiding duration (s) in *Podarcis melisellensis* (PM) and *Podarcis siculus* (PS), shown for individuals that chose to hide. Hidden lizards were observed until re-emergence, up to a maximum of 300 s; animals still concealed at that limit are right-censored and are plotted at 300 s, where both whiskers terminate. Data are presented as the median (central line), interquartile range (IQR, box), and range within 1.5 times the IQR (whiskers); no value fell beyond the whiskers, so no outliers are shown.

3.4 Intraspecific signalling

I quantified the visual signals of the lateral blue spots—traits hypothesised to function as status signals relevant to intraspecific aggression and mate choice—using a *Podarcis*-specific tetrachromatic sensor model to calculate Just Noticeable Differences (JNDs).

Analysis of chromatic contrast revealed significant sexual dimorphism ($p = 0.026$) and species divergence ($p = 0.003$; Table 6). Males exhibited significantly higher chromatic contrast than females, with an estimated increase of +1.06 JND for males, indicating that these spots are more spectrally distinct against the brown flank in males. Species identity was

also a significant predictor; PS spots showed higher chromatic contrast (+1.37 JND) compared to PM. The species-by-sex interaction was not significant ($p = 0.082$). Geographic location did not significantly influence chromatic contrast ($p = 0.77$); this signal therefore appears conserved across locations.

Luminance contrast, representing perceived brightness, was strongly influenced by sex. Males exhibited significantly higher luminance contrast than females ($p = 0.013$), with males adding approximately +3.61 JND to the contrast signal. Unlike chromatic contrast, there was no significant difference between species ($p = 0.26$) or locations ($p = 0.57$) for luminance (Table S12).

Table 6. Conspicuousness of the lateral blue flank spot expressed as Just Noticeable Differences (JND) against the surrounding brown flank using a *Podarcis* visual model. Estimates are model coefficients (positive = higher contrast). (N = 60). Significant effects ($p < 0.05$) are shown in bold.

Response	**Predictor**	**Estimate (JND)**	**p**
Chromatic contrast (dS)	Sex (M–F)	+1.06	**0.026**
	Species (PS–PM)	+1.37	**0.003**
	Species × Sex	–	0.082
	Location	–	0.77
Luminance contrast (dL)	Sex (M–F)	+3.61	**0.013**
	Species (PS–PM)	–	0.26
	Location	–	0.57

3.4.1 Visibility to predators

The luminance contrast analysis for the brown patch (lower back) revealed significant species differences in modelled visibility to predators (Table S17). For models based on visibility to bird predators, significant species effects were observed for anthropogenic ($p = 0.035$), stone ($p = 0.011$), leaf ($p = 0.016$), grass ($p = 0.004$), and ground ($p < 0.001$) backgrounds. Similarly, for models based on visibility to snake predators, significant species effects were found for anthropogenic ($p = 0.030$), stone ($p = 0.009$), leaf ($p = 0.017$), grass ($p = 0.026$), and ground ($p = 0.001$) backgrounds. PM exhibited higher luminance contrast values than PS on anthropogenic and stone backgrounds, whereas PS showed higher luminance contrast values than PM on leaf, grass, and ground backgrounds. Sex and location had no significant effect on luminance contrast of the brown patch (Table S17).

Chromatic contrast analysis for the brown patch revealed no significant species or location differences; however, PS consistently exhibited higher chromatic contrast values than PM across habitat background components. Significant sex effects were detected, with males exhibiting higher chromatic contrast than females. In models based on visibility to bird predators, this effect was significant on anthropogenic ($p = 0.042$), branch ($p = 0.046$), stone ($p = 0.040$), leaf ($p = 0.019$), and grass ($p = 0.028$) backgrounds. In models based on visibility to snake predators, all habitat background components showed significant sex effects: anthropogenic ($p = 0.048$), branch ($p = 0.047$), stone ($p = 0.047$), leaf ($p = 0.040$), grass ($p = 0.041$), and ground ($p = 0.047$).

The luminance contrast analysis for the green patch (upper back) revealed highly significant species differences across all habitat background components under both the bird and the snake visual models (Figure 15). In models based on visibility to bird predators, significant species effects were recorded for anthropogenic ($p = 0.003$), branch ($p < 0.001$), stone ($p < 0.001$), leaf ($p < 0.001$), grass ($p < 0.001$), and ground ($p < 0.001$) backgrounds. In models based on visibility to snake predators, significant species effects were recorded for anthropogenic ($p < 0.001$), branch ($p < 0.001$), stone ($p = 0.002$), leaf ($p < 0.001$), grass ($p < 0.001$), and ground ($p < 0.001$) backgrounds. PM had higher luminance contrast than PS on anthropogenic and stone habitat background components, whereas PS exhibited higher luminance contrast on branch, leaf, grass, and ground habitat background components. Sex had significant effect on luminance contrast: females exhibited higher values than males on

anthropogenic and stone backgrounds in models based on visibility to bird predators ($p = 0.028$ and $p = 0.021$, respectively) and to snake predators ($p = 0.037$ and $p = 0.009$, respectively).

Significant location effects were further analysed with post-hoc comparisons (Table S18). In models based on visibility to snake predators, Pag lizards did not differ from Sinj on anthropogenic backgrounds but had higher contrast than Knin ($p = 0.027$). On branch backgrounds, Pag lizards had higher contrast than Sinj ($p = 0.019$) but did not differ from Knin. On leaf backgrounds, Pag lizards had lower contrast than both Sinj ($p = 0.015$) and Knin ($p = 0.045$). On grass backgrounds, Pag lizards also had lower contrast than both Sinj ($p = 0.010$) and Knin ($p = 0.028$). In models based on visibility to bird predators, Pag lizards had lower contrast than both Sinj ($p = 0.016$) and Knin ($p = 0.049$) on branch backgrounds. On stone backgrounds, Pag lizards had higher contrast than both Sinj ($p = 0.029$) and Knin ($p = 0.018$). On leaf and grass backgrounds, Pag lizards had lower contrast than Sinj ($p = 0.036$ and $p = 0.029$, respectively), but did not differ significantly from Knin. These comparisons indicate that Knin and Sinj were often similar, while Pag frequently differed from one or both inland locations, particularly on vegetation-related backgrounds (Table S18).

Under chromatic contrast, the green patch exhibited highly significant species differences across all habitat background components under both the bird and the snake visual models, with PS consistently showing higher chromatic contrast values than PM. In models based on visibility to bird predators, significant species effects were recorded for anthropogenic ($p = 0.001$), branch ($p = 0.003$), stone ($p = 0.001$), leaf ($p = 0.002$), grass ($p = 0.003$), and ground ($p < 0.001$) backgrounds. In models based on visibility to snake predators, significant species effects were observed for anthropogenic ($p = 0.012$), branch ($p = 0.012$), stone ($p = 0.012$), leaf ($p = 0.020$), grass ($p = 0.018$), and ground ($p = 0.016$) backgrounds. There were no significant sex or location effects on chromatic contrast of the green patch. These results indicate that PS consistently displays higher colour-based visibility in the green dorsal patch across habitat background components, independently of sex or location.

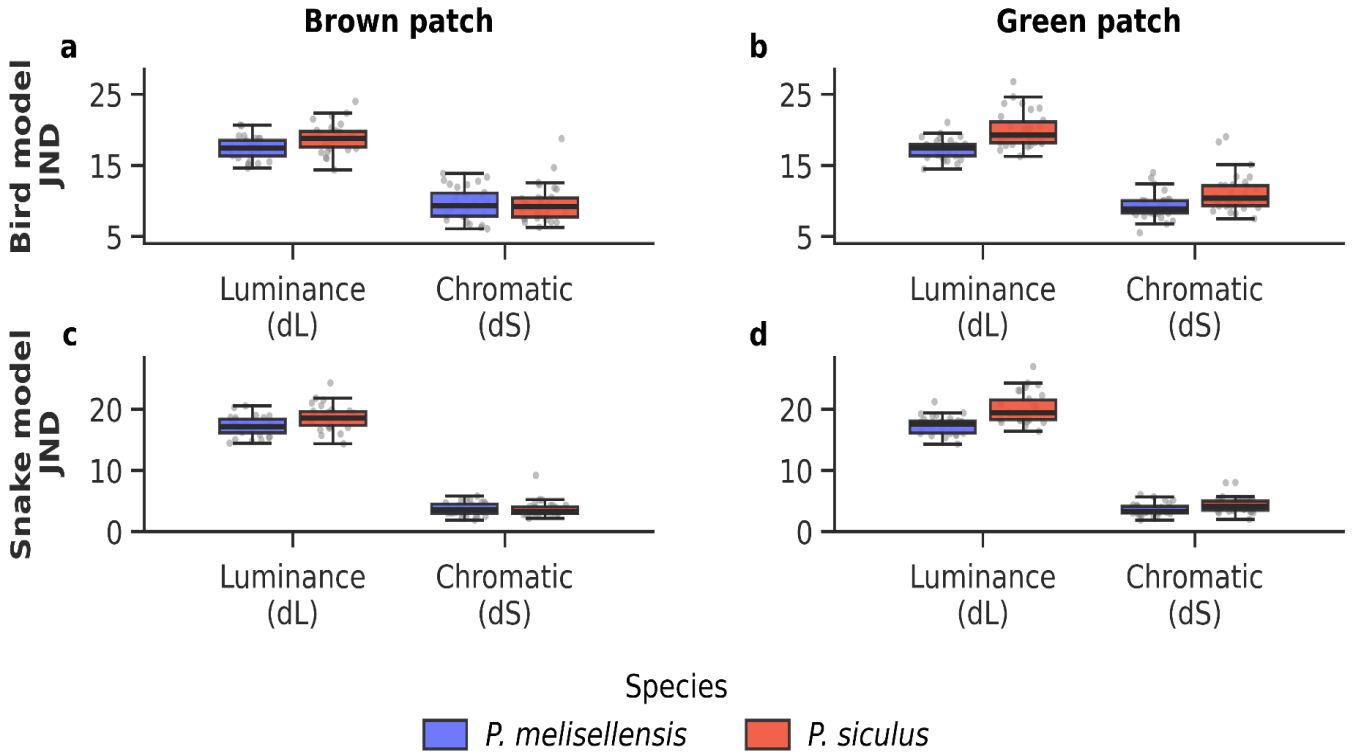

Figure 15. Just Noticeable Difference (JND) values of body patches of *Podarcis melisellensis* and *Podarcis siculus*. a, c) brown (lower back) patch; b, d) green (upper back) patch; a, b) under the bird visual model; c, d) under the snake visual model. Values are shown across averaged habitat background components, for both luminance (dL) and chromatic (dS) contrast. Data are presented as the median (central line), interquartile range (IQR, box), range within 1.5 times the IQR (whiskers), and individual data points shown with horizontal j itter. Values ≥ 1 JND are considered visually discriminable by the receiver.

Across the three anti-predator measures (flight initiation distance, flight distance and hiding duration), PS initiates escape earlier (higher FID) and flees longer distances than PM. PM showed a more condition-dependent pattern: its FID varied with location (lowest at Pag) and covaried with measured visual contrast against habitat background components. Hiding duration showed no significant differences between species or with sex, location, or time of day. In the visual models, PS is generally more chromatically conspicuous. PM, specifically lizards from Pag, exhibits lower luminance contrast on vegetation and branch backgrounds. This reduced visibility parallels the closer predator approach tolerated by PM (lower FID), although a causal link between background visibility and FID was not tested.

3.5 Dorsal pattern variation and camouflage

3.5.1 Camouflage effectiveness

The composite camouflage score (weighted ICSI, GMSD, LBP) was significantly influenced by background image category ($p < 0.001$) and species ($p = 0.030$), whereas the location effect was not significant ($p = 0.051$; Figure 16). Sex did not show a significant main effect on camouflage scores ($p = 0.139$). The most complex result was a highly significant three-way interaction between species, location, and background image category ($p < 0.001$). Significant two-way interactions were also detected between species and background image category ($p < 0.001$), location and background image category ($p = 0.027$), and sex and background image category ($p = 0.043$). In contrast, the interaction between species and location was not significant ($p = 0.990$) (Table S19).

Post-hoc tests showed that differences between PM and PS depended strongly on location and background image category. Significant differences were primarily observed in the Pag location, where PM showed higher camouflage scores (better match) than PS on complex ($p < 0.001$) and vegetation backgrounds ($p < 0.001$), as well as on bark backgrounds ($p = 0.027$), while PS scored higher than PM on anthropogenic backgrounds ($p = 0.007$). A similar pattern occurred in Knin, but only on bark backgrounds ($p = 0.024$). In contrast, no significant species differences were detected in Sinj across any background image category (Table S20).

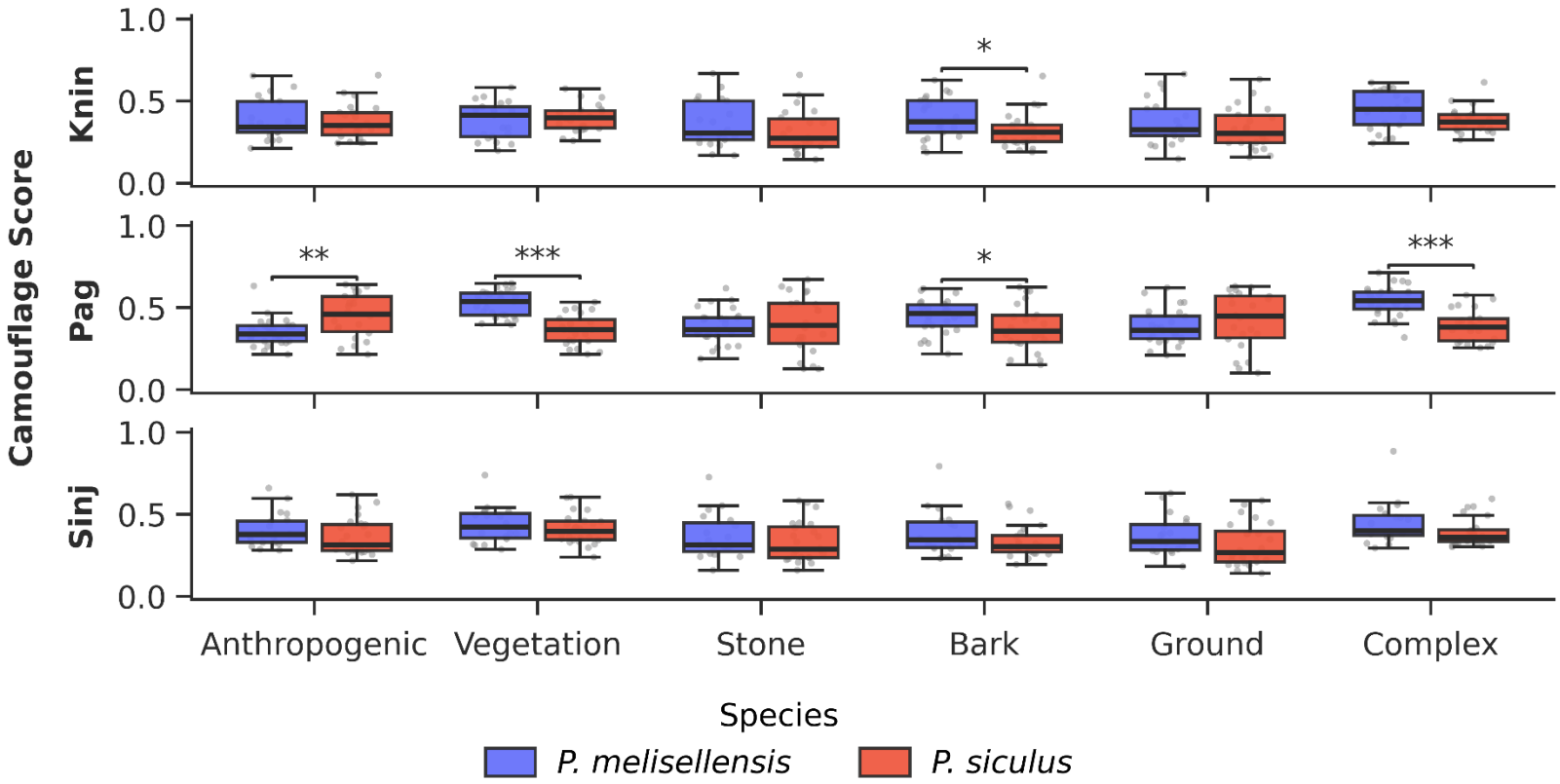

Figure 16. Composite camouflage score (weighted ICSI, GMSD, LBP) of the dorsal pattern of *Podarcis melisellensis* and *Podarcis siculus*, shown across different background image categories (Anthropogenic, Vegetation, Stone, Bark, Ground, Complex) for the three sampling locations (Knin, Pag, Sinj). Higher scores indicate a better visual match between the lizard's dorsum and the background. Based on 135 photographs, each scored against all six background categories. Data are presented as the median (central line), interquartile range (IQR, box), range within 1.5 times the IQR (whiskers), and individual data points shown with horizontal jitter. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

3.5.2 Dorsal pattern variation

Random Forest classification based on the dorsal-pattern deep features (extracted by ResNet50 from the standardised dorsal photographs) separated the two species with a balanced accuracy of 89.7% (±6.8% SD; Figure 17), substantially exceeding the 50% chance level expected for two groups. The same dorsal-pattern features could also moderately distinguish between sexes, with an accuracy of 69.5% (±8.3%), also above the 50% chance level (Table S21).

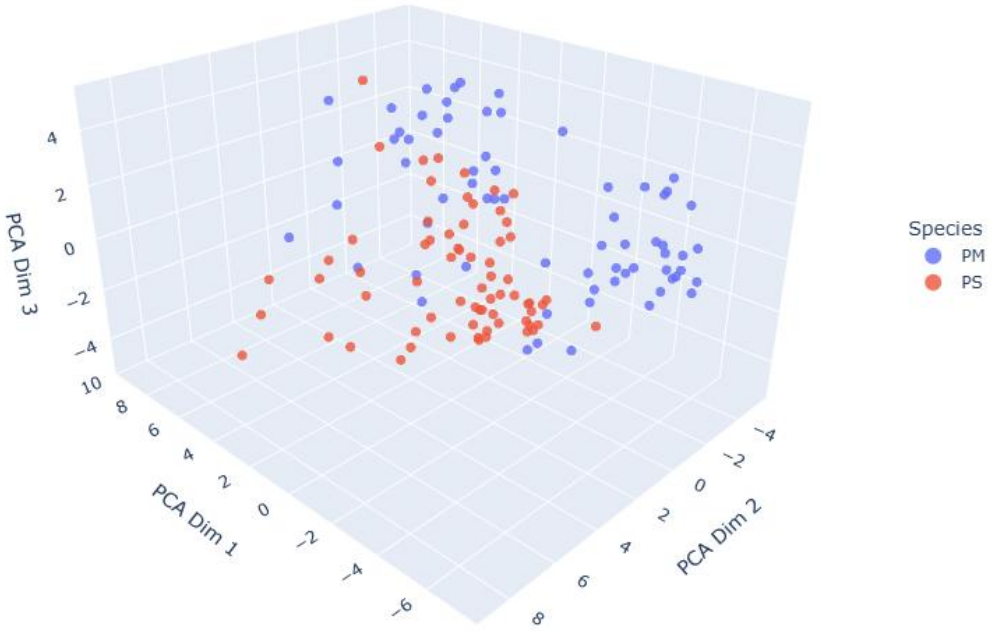

Figure 17. Three-dimensional scatter plot of the first three principal components (PCA Dim 1–3, as labelled on the axes) obtained from deep features (ResNet50) extracted from dorsal pattern images of *Podarcis melisellensis* (PM) and *Podarcis siculus* (PS). Each point is a single individual.

Classifying the four species-sex combinations yielded moderate accuracy (60.5% ±4.3%), clearly surpassing the 25% chance level. Discriminability was lower for location; the model achieved 54.4% (±5.3%) accuracy, which was above the 33.3% chance level for three groups

but indicated considerable pattern overlap among locations. Similarly, classifying the six species-location combinations resulted in lower accuracy (51.5% ±8.6%), though still high above the 16.7% chance level. The models struggled most with finer groupings: distinguishing between the six sex-location combinations yielded an accuracy of 36.1% (±8.8%), and classifying the full set of twelve species-sex-location groups resulted in 32.9% (±8.2%) accuracy. Although these values exceeded their respective chance levels, they indicate that dorsal pattern features contain limited unique information for reliably separating individuals based on more complex combined factors.

PERMANOVA analysis based on Euclidean distances between individuals in the 100-dimensional PC space revealed significant differences in pattern centroids for all main factors: species ($p = 0.001$), sex ($p = 0.001$), and location ($p = 0.001$). All interaction terms were also significant, including species × sex ($p = 0.001$), species × location ($p = 0.001$), sex × location ($p = 0.001$), and the three-way interaction between species, sex, and location ($p = 0.001$). However, the pseudo-R^2 values showed that single factors explained only a small proportion of total pattern variation: species explained 3.1%, sex 1.6%, and location 2.9%. In contrast, combinations of factors explained more variation, particularly the species × location interaction (9.5%) and the full three-way interaction involving species, sex, and location (14.4%). The Random Forest and PERMANOVA results therefore describe different quantities. The Random Forest tested whether many dorsal-pattern variables could classify individuals into groups. PERMANOVA tested how much of the total multivariate variation was explained by those groups. Species could be classified well even though species alone explained only 3.1% of total pattern variation, because most variation remained among individuals within the same species (Table S22).

PERMDISP analysis showed no significant differences in multivariate dispersion, indicating that the amount of within-group pattern variability was similar between species ($p = 0.181$), between sexes ($p = 0.262$), and among locations ($p = 0.446$). Variability did not differ significantly among species-sex groups ($p = 0.085$) or sex-location groups ($p = 0.098$), and no other interaction terms showed significant differences in dispersion. Thus, while PERMANOVA indicates that the average patterns of groups differ, PERMDISP suggests that the overall degree of pattern variability within groups is broadly similar (Table S23).

Dorsal camouflage effectiveness depended strongly on the interaction between species, location, and background image category. PM from Pag showed higher camouflage scores than PS on several backgrounds. This suggests a stronger local match between dorsal pattern and habitat. Machine-learning analyses confirmed that dorsal patterns differ most clearly between species, and to a lesser extent between sexes and locations. PERMANOVA further showed that average pattern features differ significantly among biological groups, especially when species, sex, and location are considered together. The significant PERMANOVA combined with a non-significant PERMDISP indicates that groups differ mainly in their average (mean) pattern features rather than in how variable their patterns are.

4. Discussion

This study compared sympatric *Podarcis melisellensis* and *Podarcis siculus* across movement, novelty response, aggression and signalling, escape, and camouflage. *P. melisellensis* moved in short bursts separated by frequent pauses, contacted novel objects later and less often, and rarely escalated between-species encounters although its males escalated within-species ones. Its blue flank spot was of lower chromatic contrast under the *Podarcis* visual model, it tolerated closer approach before fleeing over shorter distances, and it matched its background well only at some sites, most clearly at Pag. *P. siculus* showed the opposite tendency on each axis: fewer, longer movement bouts with sharper turning, earlier and more frequent contact with novelty, the highest aggression of any group tested in its males, a more separable flank signal, earlier and longer flight, and no comparable local camouflage advantage.

P. melisellensis (PM) and *P. siculus* (PS) occur in sympatry across all three sampled sites. They did not differ in whether the measured behaviours occurred but, in their timing, and context: how movement was distributed between bursts and pauses, how soon a novel object was contacted, how readily contests escalated, and how far approach went before flight. In parallel, the two species differed in their visual traits: how separable the blue flank spot was from the surrounding flank, and on which backgrounds the dorsal pattern matched the substrate. These differences are interpreted here as two species-level exposure profiles. Each profile groups the measured traits by their function in relation to a shared problem (visible exposure during action) rather than by what causes them at the level of development, physiology, or genetics. This framing claims only a shared ecological task, not a shared developmental or genetic mechanism [260, 261, 262, 263]. The two profiles are described separately before the species are compared and the consequences for coexistence are considered.

4.1 Exposure profile of *Podarcis melisellensis*

Across the measured behavioural axes — movement, novelty response, aggression, and escape — PM delays the actions that raise its visual exposure, and the value of each delay depends on its dorsal concealment. A PM lizard can remain on a surface, near an unfamiliar object, or near another lizard without yet doing any of the things that sharply raise its exposure. Moving in a sustained, visible way breaks background matching [297], touching an

unfamiliar cue converts caution into sampling, that is, time and movement spent investigating a cue of unknown value [142], and escalating an encounter into open contest makes a dyad conspicuous [202]. I refer to these three steps as costly actions. PM is not an inactive species: it moves, flees, enters refuges, contacts novel objects and escalates in within-species encounters. The profile describes how late in an encounter each of these steps is taken and how restricted the conditions are under which it occurs.

4.1.1 Movement

The PM movement pattern is a stable species characteristic rather than a response to novelty, because the intermittent structure of its locomotion persisted across arena contexts and was repeatable within individuals (Table S25); it is this organisation, not the amount of movement, that distinguishes PM [298, 299]. The pattern is consistent in expression and flexible in timing, a combination considered below as behavioural flexibility [161, 162].

PM is therefore better described as moving discontinuously, the burst-and-pause locomotion described for other lacertids [135, 136, 137, 138]. The distinction matters because intermittent movement changes how long the body remains visibly displaced; the pauses alone do not conceal the animal. PM therefore reduces continuous motion cues without reducing its behavioural repertoire.

The intermittent pattern also has a cost. Movement governs search and encounter opportunity [300]. Repeated pauses reduce continuous visual change, but they also slow access to food, refuges, social information and novel cues. The pattern is therefore most advantageous when the cost of pausing is low; when rapid search or exploitation is decisive, the same pattern reduces PM's access to resources.

4.1.2 Novelty response

Contact with a novel object and the suppression of movement after its appearance reflect different decisions: contact marks the first sampling of the object [142], whereas reduced movement indicates how strongly a familiar arena is again treated as uncertain [139]. In PM the two dissociated — delayed or absent contact was uniform across sites, whereas the suppression of movement varied among them and was strongest at Knin — which suggests

that delayed sampling is a disposition expressed across habitats, while the strength of the uncertainty response is adjusted locally.

The cause of the stronger suppression at Knin cannot be identified from the present data. The sites differ in climate and vegetation (Knin and Sinj are submediterranean while Pag is transitional to Mediterranean conditions), and predation pressure was not quantified. Insularity itself can also shape novelty responses in lacertids [301].

These delays carry an information cost, because any resource or information the object represents remains unused for longer [146, 302]. Studies of exploration in unfamiliar habitats show comparable phenotypic differences in how readily individuals engage new space [303]. The latency and movement-suppression patterns place PM among the more neophobic squamates studied, comparable to the tokay gecko, which hesitates to attack novel prey, feed near unfamiliar objects or enter novel space [146], and consistent with previous work on *Podarcis melisellensis*, in which neophobia toward novel foraging objects was retained even in low-predation island populations [301]. In the present test the effect was located specifically at the contact decision: PM delayed physical contact with the object while continuing to move through the arena.

4.1.3 Aggression

The distribution of escalation in PM follows the prediction of contest theory that animals escalate where the expected payoff outweighs assessment costs and injury risk [304, 305]. Conspecific males are the opponents with which PM overlaps most in food, basking sites and mates, and they were the only opponents against which PM males regularly went beyond display (Figure 6); within-species escalation thus represents intraspecific competition for the same resources. The fuller contest behaviour that species-recognition signals elicit toward conspecific opponents [306] is consistent with the same asymmetry.

The trials used unfamiliar, sex-matched animals, no residency, and a central heat source drawing both lizards toward the same spot; under those conditions the result does not mean PM is generally less aggressive.

Low between-species escalation has several candidate drivers, and each is plausible in *Podarcis*. Resource value is one, since animals should pay contest costs in proportion to what the resource is worth [307, 308], and escalation is only one of several possible outcomes of an encounter [309]. A single heat source in an unfamiliar arena may not have justified a contest with an opponent that is not a competitor for mates. Species recognition is another, since aggression is commonly tuned to opponents that compete for the same resources and mates [306, 310], and the visual and chemical cues that identify a conspecific rival are absent in a heterospecific opponent. Residency is a third, and in *P. melisellensis* specifically it changes aggression. In staged trials, residents directed more aggression toward another lizard species (*Dalmatolacerta oxycephala*) than toward their own [310]. The earlier laboratory work on this species pair was also conducted under conditions resembling residency [9, 107]. A fourth possibility is motivational asymmetry in an arena that belonged to neither animal.

The present design cannot discriminate among these drivers, because low resource value, species recognition, motivational asymmetry and the absence of residency all predict the same observation; the design features required to separate them are considered among the limitations of the study.

The spatial data support this context-dependent interpretation, because dyadic encounters can be regulated by where the animal positions itself and not only by whether it attacks [311], and PM's use of the arena depended on opponent type rather than indicating withdrawal: PM pairs closed the distance to the centre and to each other only when the opponent was a conspecific. Two interpretations of this closing of distance are possible. It may reflect contest-related approach, in which same-species rivals are worth the cost of engaging and so are approached rather than avoided; or it may reflect the absence of the avoidance that a between-species opponent elicits, leaving the animals to use the arena more evenly. The present design cannot separate the two, because the arena offered no resource to contest and no refuge to retreat to, and the distance measures were recorded without reference to which animal moved. The data do establish, however, that PM adjusted its use of space according to opponent type rather than withdrawing from the encounter.

4.1.4 Escape and refuge use

PM's escape decisions lie at the risk-tolerant end of the optimal-escape trade-off [186, 193, 194, 196, 312]: close approach is tolerated, and flight, once initiated, is short. This should not be interpreted as a weak anti-predator response. In terms of boldness, defined as the willingness to remain exposed as a threat approaches, the tolerance is specific to the anti-predator context, because the same animals contacted novelty late and escalated rarely.

The tolerance is best interpreted in relation to concealment and cover, since it was greatest where PM's camouflage was also most effective, at Pag (Table 4; Figure 16), and since it tracked PM's visual contrast against the background in a direction that depended on the surface (Table 4). Delayed flight is therefore most plausible where local visual conditions reduce the cost of remaining in place, rather than being a general property of the species.

When immobility and background matching still reduce detection, delayed flight can remain part of anti-predator behaviour rather than a failure to respond [192]. Related horned-lizard work shows that crypsis does not remove risk assessment from escape decisions [190]. PM conforms to this interpretation.

The species-specific component of PM's anti-predator response lies before refuge entry: once an animal had hidden, the time it remained hidden was unrelated to any measured predictor, whereas the decision to hide depended on time of day and local context. This is consistent with previous work on *Podarcis lilfordi*, in which FID, distance fled and hiding time were modulated by perceived predation pressure more than by baseline species traits [313], and with the wider finding in Balearic *Podarcis* that FID varies with current predation pressure across populations [314].

Within-species variation in PM shows a comparable effect, since differences in body size and shape among individuals translate into differences in field escape behaviour and microhabitat use, with clear divergence between the sexes [113].

4.1.5 Camouflage and visual exposure

For PM, concealment is determined by the background against which it rests. This is expected, because a dorsal pattern conceals only against a background and through a

particular visual system [198, 245], so the composite camouflage score measures a match between animal and surface rather than a property of the animal alone.

PM is therefore conditionally rather than generally cryptic: its pattern provides visual protection on structurally complex and vegetated surfaces and little on bare rock, a ranking of surfaces that held at all three sites and was most pronounced at Pag (Figure 16; Table S19).

This conclusion bears directly on the movement pattern. PM's stop-start movement creates repeated opportunities for concealment, but a pause only converts into concealment if the animal happens to stop on a surface its pattern matches [198, 245]. On complex and vegetated ground those opportunities are frequent; on bare stone they are not.

This kind of background dependence has also been shown in other *Podarcis* species. In *P. erhardii*, dorsal concealment changed with resting background, with individuals less detectable under avian visual models on some backgrounds than on others and with the effect differing among local contexts [315]. A dorsal pattern can reduce detection on one surface and not on another, so the surface chosen by the animal changes how well the pattern conceals it [221].

The basis of the Pag difference cannot be identified from the variables measured. Pag is the island site and the only one transitional to Mediterranean conditions, with vegetation elements absent from the submediterranean mainland sites, so the range of backgrounds available to a resting lizard plausibly differs there. Habitat backgrounds and substrate use were not quantified, however, and the predator fauna was not censused; the Pag result is therefore reported as a local pattern whose cause remains undetermined.

The models based on visibility to predators do not support a general camouflage claim either. Chromatic and luminance contrasts varied with background type, body region and predator model, so PM cannot be described as generally less visible to predators; an immobile PM reduces its exposure only when the background lowers its visual separation.

4.1.6 Synthesis

The same pattern carries both a benefit and a cost. Delay preserves position, interrupts motion cues and keeps encounters below the level of overt contest, but it is advantageous only while

the resource in question remains available. Where access is decided by speed, the same delays slow search, leave harmless novel cues unsampled and forfeit contested resources. The trade-off framework predicts this coupling: a trait that lowers one exposure cost tends to raise another [316]. The profile is a species-level pattern, a coherent set of small shifts in timing, magnitude and context rather than a single bold–shy axis, and it corresponds to the behavioural flexibility noted for the movement pattern [161, 162]. The PM profile exchanges speed of access for retained options.

4.2 Exposure profile of *Podarcis siculus*

The PS profile is defined primarily by timing: PS shortens the interval between the detection of a cue — a visual stimulus, a novel object, a conspecific — and the response to it, whether movement, contact, signalling, attack or flight.

4.2.1 Movement

PS should not be described simply as more active than PM. Its species-typical feature is the continuity of movement — few transitions between movement and stillness combined with sharper turning — which persisted across contexts and was repeatable within individuals (Table S25), whereas the amount of movement varied with context. This structure resembles the continuous search of actively foraging lacertids [137, 138].

This continuity increases visual exposure [297] but also search and encounter rates [300]. That profile matches direct comparisons in which invasive *P. siculus* is bolder and more exploratory than sympatric native congeners [117] and differs in activity and exploration among populations and habitats [109]. For *P. siculus*, the activity and exploration descriptors used here — distance moved and angular velocity — retain substantial among-individual variation and a repeatable, species-typical structure even in recently founded island populations [118].

4.2.2 Novelty response

PS gained information at the cost of exposure: it usually contacted the object well within the trial and returned to it repeatedly, males sooner and more often than females, and it held its

turning rate rather than suppressing movement once the object had appeared — it sampled the object before the cue's value was known [302].

PS's engagement with novelty is less tied to local conditions than its concealment is, since object contact was uniform across sites whereas dorsal concealment was not; this is consistent with rapid engagement, in which contact occurs before local conditions can modify the response. In two-species trials, invasive PS approached and exploited novel foraging tasks faster than native congeners and secured priority access to food [102], with exploratory behaviour predicting competitive success [117].

4.2.3 Aggression

PS aggression was a resource-based contest decision organised around sex and encounter context, not a general disposition. It was PS males who went beyond display — in most within-species trials and about a quarter of between-species ones, whereas females rarely did (Figure 6) — and their output peaked where sex and contest value coincided, in male within-species trials, with bites the commonest act and concentrated into short time windows (Figure 7); they also had the shortest latency to a first aggressive act of any group tested.

The latency result supports the interpretation of rapid engagement, which matters because contests proceed through assessment and escalation and not only through their final occurrence [304, 305]. PS decreases the time between proximity and overt action, especially in males and in within-species contests where the value of the contest is more direct [309, 317].

The arena design limits the inference. In lacertids, residency can affect the motivation and outcome of contests [318]. Under the test conditions PS males readily converted proximity into overt aggression, but this should be interpreted as context-dependent arena behaviour, varying in intensity with encounter type and sex, not as evidence that PS is always aggressive in field encounters.

Spatial behaviour provides a contrast. Dyadic encounters can be resolved by spacing rather than attack [311]. In the arena PS did not vary its distance from the centre by encounter type, so the PS result is not a simple change in arena use driven by opponent type; spatial

withdrawal and displacement from the centre do not reliably index engagement, whereas male aggressive output and shorter latency do [309, 311]. The high, escalated aggression of *P. siculus* males is consistent with the territorial behaviour reported for this species, in which residency and body-size asymmetry, rather than colour, determine the winner of staged contests [271].

The sexual dimorphism of the lateral blue spots, which are more conspicuous in males under the *Podarcis* visual model, parallels the male-biased contest behaviour without being shown to cause it.

4.2.4 Escape and refuge use

PS's escape response is species-typical rather than site-specific, since neither flight initiation nor flight distance was structured by site, sex or habitat background (Table 5): PS converts approach risk into distance early and continues to flee farther once flight has begun.

This is consistent with the visual component of the profile and should not be reduced to fearfulness. Earlier flight in PS is best interpreted as a rapid transition from exposure accepted for access to exposure avoided as danger. PS thus responds earlier in both directions: it samples objects and initiates aggression sooner, the rapid engagement also reported as greater boldness and exploration in this invasive species [117], and it also leaves earlier and flees farther from an approaching predator. Risk-taking in PS is therefore context-specific: it approaches novelty and rivals readily but responds cautiously to predators, so that no single boldness ranking applies across contexts.

The visual models help explain why remaining in place during approach may be less safe for PS. The reasoning that allows a cryptic animal to delay flight [190, 192] does not apply to PS, whose dorsal colouration provides little measured visual support for holding position during approach [198, 245].

Among PS individuals that entered a refuge, hiding duration was not predicted by any measured variable, which is consistent with emergence decisions governed by lost surface time and thermal opportunity rather than by species identity [197, 319]. The anti-predator difference shown by PS therefore lies in flight rather than in refuge use.

4.2.5 Camouflage and visual exposure

PS is not without camouflage; its concealment depends primarily on the surface against which it rests. What distinguishes PS is that its ranking of surfaces was not constant among sites, which accounts for a substantial part of the species × location × background interaction (Table S19): the surfaces it matched best at Pag, anthropogenic and bare ones, were those it matched worst at Knin and Sinj (Figure 16).

In the predator visual model's PS's chromatic separation from the background, carried mainly by the green dorsal patch, was high and largely independent of substrate, whereas its luminance separation depended on substrate and body region. PS is therefore not uniformly conspicuous, but its concealment is not supported by local background matching; the profile is maintained across sites at the cost of greater visual exposure.

4.3 Coexistence

4.3.1 What separates the two species

Neither species lacks any behaviour or visual trait that the other possesses. Both move, sample novelty, escalate, flee and hide, and both carry a cryptic dorsum and a blue flank signal; the profiles differ in when, and under which conditions, each of these is expressed. The contrasts between the species are therefore interpreted as differences in timing and context rather than in kind, and the questions are whether the contrasts are sufficiently stable and consistent in direction to be treated as species-level profiles, and how they depend on context.

The contrasts are stable. The organisation of movement that distinguishes the species — PM's many short bouts against PS's fewer, longer and sharper-turning runs — did not depend on whether the arena was new, familiar or held a novel object, and it was repeatable within individuals of both species to a similar degree (Tables S1, S25); only the amount of movement, its distance and duration, shifted with context. Body size moved individuals along the same continuity axis without accounting for the species contrast, which held with size as a covariate, and sex shifted tempo and contact latency in both species alike without touching it; condition, limb proportions, sampling year and time of testing explained almost nothing. The same holds for contests, where neither site, year nor body shape altered the timing or output

of aggression (Tables S6–S11), and for the flank signal, which separated the species in the same way at all three sites (Table 6). Even the dorsal pattern, the most variable trait measured, is species-diagnostic: deep image features told the species apart far more reliably than they told apart sexes or sites, although species accounted for only a small share of the total variation and within-species variability was the same in both (Tables S21–S23). The species-typical pattern is thus a shift in the average within broad individual variation, which is the variation on which local background matching depends.

The contrasts are also consistent in direction. On every behavioural axis PS acted first: it reached the novel object sooner and returned to it more often, turned proximity into a first aggressive act sooner in both encounter types, and started to flee at a greater distance before fleeing farther, by a margin that differed between the sexes (Tables S4–S7, S13, S14). Escalation was male biased in both species, but PM males went beyond display only against conspecifics, whereas PS males did so against both species, so the contest asymmetry is one of timing and output, not of capacity to fight. The visual traits point the same way: PS's flank spot has the higher chromatic contrast under the *Podarcis* visual model, and its green dorsal patch the higher chromatic contrast against every background under both predator models, whereas luminance contrast depended on substrate in both species, each being more conspicuous on the surfaces that the other matched (Tables 6 and S17). Early action and higher visual availability therefore coincide in one species, and delay and lower visual availability in the other, as the exposure framework predicts.

These two results — a more separable flank signal and faster, higher male contest output in PS — should not be combined into a causal link from colouration to aggression. They indicate greater signal availability and faster escalation in the same species, in the same arena, without showing that the first caused the second. Colour patches affect interaction only when a receiver can separate them from the surrounding body surface [202], and residency and size shape contest outcomes independently of colour [318]; in *P. muralis*, body size predicts contest outcome better than UV colour alone [320], and in *P. tiliguerta* UV-blue patch traits correlate with size-related male traits [321]. A causal test would require manipulating the patch — by paint or filter — under matched arena conditions, which this design did not include. What can be said is that PS presents receivers with a more distinct chromatic cue, and that the claim is limited to conspicuity, with no demonstrated advantage in dominance, mating success, or fighting ability.

Context affects the two species asymmetrically. PS's novelty and escape responses were the same at every site, whereas PM's flight initiation was tuned both to site and to its own visual contrast against the background, and PM's neophobic response was strongest at Knin. Concealment depended on background in both species but not in the same way at the same places: PM's advantage was broad at Pag, reduced to bark at Knin and absent at Sinj, and at Pag PS's own best surfaces shifted to anthropogenic ground (Tables S19, S20). Once in refuge the asymmetry disappears: hiding duration was unrelated to any measured predictor in either species, although the decision to hide at all varied with time of day and with local combinations of sex and site. The species difference is therefore carried by what happens before refuge is reached, and it is the PM component of the difference that is locally conditioned. The coexistence argument that follows rests on this asymmetry.

Taken together, the two species meet the same resource points with different timing. PS tends to reach, sample, and escalate sooner; PM more often keeps its position and cover until it acts. Both patterns were repeatable, so the difference is stable enough to influence repeated encounters consistently rather than averaging out [322, 323].

4.3.2 Coexistence-relevant framing

Two competitors with the same resource needs are expected to exclude one another [16], yet PM and PS co-occur at Knin, Pag, and Sinj. Coexistence theory allows persistence when differences of the kind set out above keep interspecific costs below the exclusionary threshold [46, 90]. In this system the candidate mechanism is behavioural timing at shared resource points rather than the classic partitioning of space, diet, or season described for lizard communities [108, 324].

The unit of this interpretation is the shared resource point: a refuge entrance in a drystone wall, a basking stone, a food item, a novel object, or anything else both species can use or deny within one behavioural episode [325, 326]. At the study sites such points are readily identified. The drystone walls, outcrops, and field margins where both species were caught differ in how many usable crevices and basking positions, they offer, and exclusion becomes possible where such points are scarce. This is a finer scale than habitat overlap, since a habitat patch can hold both species even when a single basking stone cannot.

4.3.3 Site-specific contexts

The three sites provide different contexts for this mechanism. At Pag, where PM's concealment was strongest, its flight initiation distance shortest and the movement of both species most fragmented and briefest, the substrate favours delay, and PM's strategy of delayed access should be most effective. Pag is also the one site where PS's concealment reordered onto anthropogenic and bare surfaces, so the two species' best resting surfaces there are not the same ones. At Knin, where both species moved longest and farthest, PM's advantage narrowed to bark while its movement suppression after novelty was strongest, caution expressed behaviourally where visual support is weaker. At Sinj no background separated the species and turning rate was highest in both; Sinj is therefore the site at which PM's delay has the least visual support and PS's continuous movement the fewest constraints.

The present evidence does not show how far these contrasts translate into site-specific coexistence conditions; the inferential limits of the site comparison are set out below.

4.3.4 Mechanisms of access at shared resource points

Access is decided first by order of arrival. The movement and novelty contrasts described above place PS at a shared point before PM in most encounters and lead to earlier use of an unfamiliar cue. Previous work indicates the value of first arrival: in a *Podarcis* food-station experiment, invasive PS reached food first, ate more, and gained more mass than native *P. virescens*, without needing aggression [102]. That was a different species pair, but it is the same mechanism the present movement and novelty results predict for PM–PS resource points. The difference here is that the later species is delayed but not excluded, and its information about the point is updated later [302].

A second route is interference below the level of biting. Displays and spacing affect movement even without biting, since a display can delay approach or divert a path to a heat source without injury [311, 326], and this is the level at which between-species interference operated in the arena, where aggression between the species stayed at displays, bites were confined to male within-species trials, and PS reached its first aggressive act sooner in both encounter types. The laboratory evidence for this species pair is consistent with that reading. Downes and Bauwens showed experimentally that PS directs aggression at PM and displaces

it from preferred basking sites [9]; first encounters shaped later dyadic access in the same pair [107]; and in another lizard system interspecific conflict changed retreat-site use and access to preferred shelters [327]. In invaded systems more broadly, PS aggression and boldness accompany the displacement of native species [102, 117]. In the field this would take the form of pressure rather than fighting, with PM yielding position, approach time or a refuge-adjacent spot while PS gains the point without paying the full cost of a contest [305, 307]. Residency, absent from the arena by design, can shift this balance in PM's favour [310].

Escape and visibility form the third route. Around a resource point PM yield less ground per disturbance than PS, provided cover is close and the background matches its pattern; on mismatched substrates the same waiting becomes exposure without protection [198, 221, 245]. Refuge structure decides how much this matters, because several entrances can accommodate both strategies, whereas a single entrance itself becomes the contested point [327]. Work on Balearic *Podarcis* shows escape thresholds tracking local predation pressure rather than species identity alone [313, 314], which fits the present pattern of a species-level FID difference with site-level modulation only in PM. Visibility links the two routes: PS is the more chromatically detectable of the two under both predator models [202], so its earlier and longer flights and its readiness to act without local background matching form a single strategy of earlier action at the cost of greater visual exposure.

4.3.5 Limits to competitive displacement

PS reaches resource points first and exerts interference below the level of biting, yet displacement has not followed at these sites. The data suggest three restraining factors. First, the sites still offer capacity: walls with many crevices and extensive basking surfaces delay access without removing it. Second, PM's waiting works where its pattern matches the substrate, most broadly at Pag, and concealment converts delay into retained position. Third, predation may tax the two strategies unequally. PS is the more visually available species under both predator models, and non-consumptive predator effects raise the cost of the movement, contact and display on which its access depends [186, 195, 297]. If predators detect and target the more conspicuous competitor more often, predation will fall more heavily on the dominant species, the condition under which predator-mediated coexistence can let a subordinate persist [231, 328, 329]. The data fully supports only the first step of this

argument, PS's greater visual availability [202] and the remainder is a hypothesis suggested by the results.

The same reasoning identifies the conditions under which coexistence should shift toward displacement: low-capacity points such as a single refuge entrance, an isolated basking surface, or one food item; mismatched substrates that strip PM's waiting of cover; and points of high contest value, which attract male PS first [307]. Because escalation is male driven in both species, the pressure PM faces at such points is earlier male PS pressure [311]. An island case illustrates the outcome when these restraints fail: invasive PS males attacked endemic males more often, native males escaped more often, and spatial exclusion was linked to reproductive loss [330]. The PM–PS thermal experiments sit between the arena and that endpoint, where interference changed thermal microhabitat use and growth [9, 107]. They indicate the course displacement would take if the capacity of resource points declined, for example through habitat simplification.

4.3.6 Inferential limits of the study design

The site comparisons are based on three locations without habitat quantification, predator censuses or density estimates. The conclusion that Pag favours PM's strategy is therefore an inference from the distribution of the measured advantages among sites, not a measured outcome. The design does establish the contact-scale processes — order of arrival, yielding, and visual detectability — and any site-specific test of PM–PS coexistence will have to operate at that level.

4.4 Limitations and future directions

4.4.1 Limitations

Several limitations bound the interpretation. The data do not show that a given PM or PS individual expresses the whole profile across tests, so the profile remains a species-level interpretation.

Behaviour and colour were not measured in the complete sample. Spectrophotometry was conducted on 60 animals from the 2021 cohort, while dorsal-pattern and camouflage analyses used standardised photographs (N = 135), whereas the behavioural analyses used both

laboratory and field samples. This prevents individual-level tests linking behaviour, dorsal pattern, and signal contrast in the same animals. A future design should measure behavioural tests, dorsal pattern, spectrophotometry in the same individuals.

Because the study describes behavioural and visual patterns rather than their selective history, it does not test whether selection produced the trait combination [258]. For example, the data show that PM and PS differ in movement continuity, blue-spot contrast, and escape distance, but not whether those differences are inherited, plastic responses to local conditions, or by-products of other traits.

The tests compared PM and PS under standardised conditions. Each test measured one part of behaviour: movement, object contact, escape, hiding, visual contrast, or dyadic aggression. The novel-object test measured contact with an unfamiliar rubber-glove object. It did not measure first use of food, a refuge edge, or a basking surface. Novel-object responses depend on object properties and test context [166] and on the response variable chosen [331]. Although PS contacted an unfamiliar object sooner and more often than PM, this does not by itself prove field resource use.

Camouflage scores and visual models estimate potential visibility, not receiver response: they do not show that predators attack more, that lizards choose matching surfaces in the field, or that receivers respond to blue-spot contrast [198, 202, 245]. The refuge variables have the same limit. FID, FD, hiding occurrence, and HD describe what happens during a human approach and after refuge entry, but they do not measure refuge quality, refuge ownership, or repeated disturbance; and a longer stay need not indicate higher perceived risk, because emergence from refuge itself carries opportunity and thermal costs [197, 319]. Because the species-level FID difference held at all three sites, it is unlikely to reflect a site-level difference in predation regime [313, 314].

The aggression trials used unfamiliar, sex-matched dyads around a central heat source. They did not include territory ownership, repeated encounters, individual recognition, mate presence, natural density, or long-term access to refuges and basking sites. Residency and size can change contest rules in lacertids [318]. Size adds a further asymmetry, since between-species pairs were matched by within-species size rank instead of absolute SVL, and PS is the larger species, so a size difference is embedded in the between-species results. Residency also

changes interspecific aggression in *P. melisellensis* [310]. Therefore, the presented results should be applied only to novel within- and between-species encounters. This design cannot fully separate the candidate drivers of low between-species escalation (resource value, species recognition, residency and motivational asymmetry); designs that assign residency roles, vary the value of the contested resource or stage encounters after familiarisation would be required.

Lizard performance and habitat use depend on the local distribution of thermal conditions and cover [332], prey and refuges also matter [333]. The present data therefore identify contact-scale differences in timing and position but cannot estimate resource acquisition in the field.

The field experiments would be enriched if there were more data on lizard microhabitat use: estimates of predator abundance, refuge density, prey availability, and thermal resource distribution at each site, together with vegetation-to-rock ratios, habitat heterogeneity, shading, and, above all, abundance and density estimates for both species at each site [334, 335]. In their absence, the present results support contact-scale behavioural comparisons between the species, but not site-level inference about habitat quality, predation pressure, or population density. The same behavioural response can therefore have different access value under different local conditions. The data support a contact-scale access hypothesis without yet showing when the measured behaviours bring food intake, heat gain, or long-term spatial control.

The three sampled populations also set a scale limit. Pag, Knin, and Sinj show useful local variation, but all three sites were sampled under PM-PS coexistence. The design cannot separate stable species differences from traits expressed under syntopy, habitat filtering, plasticity, contact history, seasonal context, or repeated PM-PS contact. For this comparison, populations of both species from areas in which they do not coexist (that is areas where only one species is present) would have been necessary, which was beyond the scope of this research. The data describe single-encounter responses, including direct between-species trials, but not how these behaviours develop over repeated or prolonged PM-PS contact.

4.4.2 Future directions

All three sampled locations were chosen because PM and PS occur together in sympatry and syntopy. That design was needed for direct comparison, but it leaves no single-species

baseline. Future sampling should add replicated PM-only and PS-only locations matched to syntopic locations for substrate, refuge density, thermal structure, predator regime, season, and habitat openness. Such sampling would provide the control needed to determine whether the measured behavioural and visual differences are stable species traits or contact-dependent expressions. If the PM pattern appears in PM-only populations, it would be a stronger candidate for a stable species profile. If it changes with PS presence, contact history, plasticity, habitat filtering, or local adaptation, those processes will have to be tested, for example by common-garden rearing or by repeated testing of translocated individuals.

Future field work should map habitats as arrays of resource points: small positions or items a lizard can gain, hold, or lose in a short behavioural interval (one refuge entrance, one high-temperature surface, one prey item, one novel object, or the space around another lizard). For each point, the field sheet could record how many animals can use it, how close cover is, how warm it is, how well the substrate matches the animal, how many arrival routes exist, and whether another lizard already occupies it. At the site scale, it should also record PM and PS abundances and densities, which this study lacked. These are the conditions under which delay preserves access or early action secures the point first [334, 335, 336].

PM's more segmented movement can reduce continuous motion cues only when pauses occur on surfaces that support matching. PS's higher-continuity movement can increase access, but it also gives predators and receivers more positional change to detect. Future field tests should track movement, stops, and substrate choice during the same event. Because continuous video tracking is rarely feasible in the field, miniature accelerometers or bio-loggers could record when each lizard moves, pauses, changes direction, approaches cover, or crosses a resource point. A mapped substrate layer could then assign each pause a background-matching score under predator and *Podarcis* visual models. The response variable would be whether a lizard pauses on surfaces where its dorsal pattern has stronger background matching, not movement or camouflage alone. Testing whether PM and PS choose surfaces by their background match would test behavioural camouflage as a real-time decision. It would also supply the evidence the access hypothesis still lacks, namely that pauses occur where concealment is effective, which is the assumption on which the PM strategy rests.

Repeated-contact designs could test whether PM changes its delay after harmless novelty, repeated displacement, or stable PS neighbours, and whether PS reduces early contact when

early sampling repeatedly carries costs. Also, future tests should include more than one pair of lizards. The aggression test used one pair and one thermal point. Natural interference can involve several lizards, several refuge entrances, several basking positions, repeated recognition, and shifting local density. A small-group design would test whether the dyadic pattern scales to local contact systems. Shared natural enemies are a further untested pathway: competing lacertids share haemogregarine blood parasites [337], so apparent competition could link PM and PS through a shared parasite or predator without direct resource competition.

The visual results remain estimates of visual opportunity rather than measured predator response and could be enhanced by receiver-side tests. Predator visual models and camouflage scores could be followed by field observations, calibrated presentation trials, or video-supported natural encounters that estimate detection, orientation, approach, or attack probability.

The neurobiological substrate of the observed behaviours could be mapped to specific neurochemical correlates. PS and PM differ in brain dopamine concentrations [130], and dopamine and other monoamines are tied to learning, motivation, reward, aversive and alerting events, exploration, and stress responses in vertebrates [338, 339, 340, 341]. These results justify monoamines as candidate predictors of movement organisation, novelty sampling, aggression timing, and risk-sensitive delay; the relationships are context-dependent, varying with stress, dominance status, behavioural state, and hierarchy formation [342, 343, 344], which could be further investigated in this model.

5. Conclusion

In this work, behavioural and visual divergence between populations of *P. siculus* and *P. melisellensis* coexisting in sympatry was assessed. PM and PS differed less in total activity than in how quickly they moved, contacted novelty, fled, or escalated. PM generally delayed the transition to overt action. PS more often converted the same situation into movement, contact, signal availability, aggression, or flight.

H1 was confirmed: *P. melisellensis* exhibited lower levels of exploratory behaviour and higher levels of neophobia than *P. siculus*. PM moved with more segments and lower angular velocity than PS across open-field contexts and contacted the novel object later and less often. Lower exploration and higher neophobia therefore did not mean PM was inactive: PM moved but delayed direct sampling of novelty and returned movement to stillness again and again. The strongest neophobic change appeared in PM from Knin, where movement duration dropped most after object introduction.

Furthermore, H2 was also partly validated: *P. melisellensis* had less conspicuous colouration and expressed lower levels of anti-predatory behaviour than *P. siculus*. PM initiated flight at shorter distances and fled shorter paths than PS. This shorter FID reflects a risk-tolerant escape strategy tied to local concealment rather than a generally weaker anti-predator response. Dorsal camouflage differed by location and background, PM had its strongest dorsal camouflage advantage at Pag, a weaker advantage at Knin, and no advantage at Sinj. Crypsis was not a fixed species property, it depended on whether the local background made the dorsal pattern harder to separate.

Conversely, H3 was partially demonstrated. *P. melisellensis* did not show stronger dominance-signalling colouration, *P. siculus* had higher blue-spot chromatic contrast under the *Podarcis* visual model, while luminance did not separate the species. Yet *P. melisellensis* showed lower aggression in both intra- and interspecific interactions than *P. siculus*. The aggression prediction was better supported. PM showed lower aggression in between-species encounters and longer latency to the first aggressive act, whereas PS males produced the strongest aggressive output, especially in conspecific male encounters. PM males did escalate in conspecific trials, so the difference was not in whether PM showed aggression but in how readily proximity escalated into overt contest.

An additional objective was to determine relevant morphological traits that are consistently associated with behaviour within and between species. Morphology gave limited support for the behavioural profiles. Colour and dorsal pattern separated the species more clearly than the measured morphological covariates.

The clearest contrast is between delaying visible or contact-heavy actions and acting early to gain access. PM delays contact, reduces continuous motion cues, waits longer before flight, flees shorter distances, and rarely turns between-species proximity into overt aggression. PS moves with higher angular velocity, samples novelty sooner, gives receivers a more separable flank signal, escalates faster in male contests, and flees earlier when approached. These differences can allow syntopy where resource points are distributed, cover is close, and there is enough room for one species to delay while the other acts sooner. They can also create local displacement where one basking point, refuge entrance, food item, or interaction space rewards earlier arrival. Syntopy therefore does not imply equal access, because access is decided at individual resource points, where timing, visibility, and contest behaviour interact. *Podarcis melisellensis* and *P. siculus* seem to have developed different activity paradigms that allow them to coexist in the Eastern Adriatic.

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7. Supplementary Materials

A. Description of locations

Field research was conducted at three locations along the Eastern Adriatic coast: the vicinity of Sinj (43.7226° N, 16.6738° E), the vicinity of Knin (44.0418° N, 16.2329° E), and on Pag Island (44.5686° N, 14.8902° E). These sites were selected as they are separated by at least 50 km to ensure the sampling of distinct populations (Figure 1). I selected locations with comparable habitat complexity, including agricultural fields, pastures, meadows, interspersed with hilly terrain featuring macchia and forest patches. Climatically, Sinj and Knin fall within the submediterranean zone, whereas Pag represents a transition between submediterranean and mediterranean climates. This difference influences vegetation. Sinj and Knin share similar submediterranean plant communities (characterised by species such as *Quercus pubescens*, *Carpinus orientalis*, and *Juniperus oxycedrus*), whereas Pag additionally incorporates Mediterranean elements such as *Quercus ilex*, *Spartium junceum*, and *Phillyrea angustifolia* within its macchia. The predator fauna was not censused, and quantitative data on predator abundance, predation pressure, refuge use and food consumption do not exist for these specific locations.

B. Inter- and intra-specific differences in behaviour between two species of lizards, *Podarcis melisellensis* and *Podarcis siculus*

Table S1. Generalized Linear Model Estimates for Behaviour Types of *Podarcis melisellensis* and *Podarcis siculus* (significant results marked bold)

Dependent Variable	Type of behaviour											
	Exploration			Activity			Neophilia			Neophobia		
	Term	Df	F	*P* - value	Df	F	*P* - value	Df	F	*P* - value	Df	F	*P* - value

Dependent Variable		Type of behaviour											
		Exploration			Activity			Neophilia			Neophobia		
Angular Velocity	Species	1	14.592	**<0.001**	1	4.314	**0.039**	1	26.825	**<0.001**	1	6.343	**0.012**
	Sex	1	1.474	0.226	1	5.902	**0.016**	1	10.07	**0.002**	1	0.783	0.377
	Location	2	5.319	**0.006**	2	3.251	**0.041**	2	6.189	**0.002**	2	0.728	0.484
	SVL	1	5.600	**0.019**	1	1.548	0.215	1	1.731	0.190	1	0.095	0.758
	Year	1	0.008	0.930	1	3.473	0.064	1	0.720	0.397	1	2.124	0.146
	Time	1	4.753	**0.030**	1	0.454	0.501	1	0.810	0.369			
	SMI							1	4.853	**0.029**			
Distance Moved	Species	1	14.590	**<0.001**	1	1.231	0.268	1	1.909	0.168	1	0.825	0.365
	Sex	1	0.553	0.458	1	0.179	0.673	1	0.000	0.985	1	0.281	0.597
	Location	2	2.718	0.068	2	**3.088**	**0.048**	2	1.051	0.351	2	0.442	0.644
	SVL	1	6.480	**0.012**	1	2.389	0.124	1	0.685	0.409	1	0.096	0.757
	Year	1	2.087	0.150	1	0.031	0.861	1	0.223	0.637	1	0.326	0.569
	Time	1	3.496	0.063	1	3.884	0.051	1	0.752	0.387			
Movement Duration	Species	1	3.773	0.053	1	0.003	0.958	1	6.704	**0.010**	1	7.225	**0.008**
	Sex	1	0.458	0.499	1	0.274	0.601	1	0.195	0.660	1	1.022	0.313
	Location	2	5.968	**0.003**	2	4.941	**0.008**	2	0.466	0.628	2	5.904	**0.003**
	SVL	1	9.199	**0.003**	1	1.878	0.172	1	1.429	0.233	1	0.001	0.975
	Year	1	1.281	0.259	1	2.345	0.127	1	0.387	0.535	1	0.235	0.628
	Time	1	2.219	0.138	1	1.486	0.224	1	0.167	0.684			
	Species: Location										2	6.207	**0.002**

Dependent Variable		Type of behaviour											
		Exploration			Activity			Neophilia			Neophobia		
Number Moving Segments	Species	1	36.596	**<0.001**	1	24.714	**<0.001**	1	53.351	**<0.001**	1	1.855	0.175
	Sex	1	0.175	0.676	1	0.02	0.888	1	0.037	0.848	1	0.093	0.761
	Location	2	4.009	**0.019**	2	6.886	**0.001**	2	12.901	**<0.001**	2	2.363	0.097
	SVL	1	3.541	0.061	1	5.281	**0.022**	1	6.49	**0.012**	1	0.008	0.928
	Year	1	0.312	0.577	1	0.389	0.534	1	0.798	0.373	1	0.062	0.804
	Time	1	1.449	0.23	1	0.081	0.776	1	0.476	0.491			

Table S2. Post Hoc Estimated Marginal Means by Location for Behaviour Types (Tukey-Adjusted) of *Podarcis melisellensis* and *Podarcis siculus* across three locations in Croatia: Knin, Sinj and Pag (significant results marked bold)

Dependent Variable		Exploration				Activity				Neophilia			
	Contrast	Estimate	SE	t - value	*P* - value	Estimate	SE	t - value	*P* - value	Estimate	SE	t - value	*P* - value
Angular Velocity	KNIN - PAG	-0.142	0.162	-0.872	0.658	-0.044	0.216	-0.203	0.978	-0.043	0.267	-0.16	0.986
	KNIN - SINJ	-0.437	0.161	-2.707	**0.020**	-0.413	0.216	-1.913	**0.013**	-0.76	0.264	-2.875	**0.012**
	PAG - SINJ	-0.295	0.174	-1.700	0.207	-0.369	0.232	-1.594	0.251	-0.717	0.287	-2.501	**0.035**
Distance Moved	KNIN - PAG					26.627	7.91	3.366	**0.003**				
	KNIN - SINJ					10.215	7.942	1.286	0.405				
	PAG - SINJ					-16.412	8.581	-1.913	0.138				
Movement Duration	KNIN - PAG	75.841	18.173	4.173	**<0.001**	51.712	21.579	2.396	**0.046**				
	KNIN - SINJ	25.281	18.175	1.391	0.347	75.34	21.691	3.473	**0.002**				
	PAG - SINJ	-50.56	19.433	-2.602	**0.027**	23.628	23.186	1.019	0.566				
Number Moving Segments	KNIN - PAG	-27.846	13.100	-2.126	0.087	-4.443	3.407	-1.304	0.394	-5.762	3.448	-1.671	0.219
	KNIN - SINJ	5.753	12.934	0.445	0.897	3.762	3.408	1.104	0.513	6.889	3.436	2.005	0.113
	PAG - SINJ	33.599	14.039	2.393	**0.046**	8.204	3.659	2.242	0.066	12.651	3.714	3.406	**0.002**

Table S3. Post Hoc Estimated Marginal Means by Location (Tukey-Adjusted) of species across location in variable Movement duration for neophobia of *Podarcis melisellensis* and *Podarcis siculus* across three locations in Croatia: Knin, Sinj and Pag (significant results marked bold)

contrast	estimate	SE	t - value	*P* - value
PM KNIN - PS KNIN	-0.322	0.120	-2.688	**0.029**
PM KNIN - PM PAG	-0.265	0.086	-3.061	**0.018**
PM KNIN - PS PAG	-0.158	0.101	-1.561	0.257
PM KNIN - PM SINJ	-0.255	0.093	-2.743	**0.029**
PM KNIN - PS SINJ	-0.363	0.119	-3.059	**0.018**
PS KNIN - PM PAG	0.057	0.128	0.447	0.701
PS KNIN - PS PAG	0.164	0.090	1.824	0.173
PS KNIN - PM SINJ	0.066	0.106	0.63	0.661
PS KNIN - PS SINJ	-0.040	0.087	-0.464	0.701
PM PAG - PS PAG	0.107	0.107	1.000	0.477
PM PAG - PM SINJ	0.009	0.095	0.102	0.911
PM PAG - PS SINJ	-0.097	0.126	-0.774	0.599
PS PAG - PM SINJ	-0.097	0.092	-1.055	0.477
PS PAG - PS SINJ	-0.205	0.089	-2.289	0.069
PM SINJ - PS SINJ	-0.107	0.105	-1.023	0.477

Table S4. Results of testing for best-fitting parametric distribution for Accelerated Failure Time model

Distribution	AIC
loglogistic	2556.810
lognormal	2559.040
exponential	2568.340
weibull	2570.310

Table S5. Model Estimates for Neophilia Behaviour Types of *Podarcis melisellensis* and *Podarcis siculus* across three locations (Knin, Sinj and Pag) in Croatia. Negative Binomial Generalized Linear Model for Contact Frequency and Accelerated Failure Time for Contact Latency (significant results marked bold)

Dependent Variable				
Contact Frequency	Term	Df	LR Chisq	Pr(>Chisq)
	Species	1	11.200	**0.001**
	Sex	1	8.099	**0.004**
	Location	2	0.206	0.902
	SVL	1	0.349	0.555
	Year	1	0.037	0.847
	Time	1	0.336	0.562
Contact Latency	Term	Acceleration factor	statistic	*P* - value
	Species	0.58	-1.980	**0.048**
	Sex	0.677	-1.980	**0.048**
	Location	1.1	0.420	0.674
	SVL	1.04	0.194	0.846
	Year	0.822	-1.120	0.261
	Time	0.998	-0.107	0.915

C. Aggression

Table S6. Latency to the first aggressive act: Cox mixed-effects model, Type III analysis of deviance (significant effects in bold).

Term	df	χ^2	Hazard ratio	p
Species (PS vs PM)	1	10.30	7.57	**0.013**
Encounter type (within vs between)	1	10.46	10.75	**0.002**
Sex (M vs F)	1	38.90	8.20	**<0.001**
Location	2	0.43	—	0.807
Year	1	3.58	—	0.059
Species × Encounter type	1	3.98	—	0.052

Table S7. Latency to the first aggressive act: pairwise post-hoc contrasts (log-hazard scale, Tukey-adjusted).

Contrast	estimate	SE	z	p
PM between – PS between	−2.389	0.744	−3.21	**0.007**
PM between – PM within	−2.405	0.744	−3.23	**0.007**
PM between – PS within	−3.205	0.728	−4.40	**<0.001**
PS between – PM within	−0.016	0.327	−0.05	1.000
PS between – PS within	−0.816	0.285	−2.87	**0.022**
PM within – PS within	−0.800	0.287	−2.79	**0.027**

Table S8. Distance from the arena centre: linear mixed model (Type III Wald F, Kenward–Roger df).

Term	F	df	df.res	p
Species	0.18	1	440.6	0.671
Encounter type	11.32	1	229.5	**<0.001**
Sex	0.01	1	225.2	0.916
Location	0.24	2	225.5	0.791
Year	1.23	1	225.0	0.269
Species × Encounter type	13.48	1	229.6	**<0.001**

Table S9. Distance from the arena centre: Tukey post-hoc contrasts.

Contrast	estimate	t.ratio	p
PM between – PS between	−4047	−0.42	0.974
PM between – PM within	29848	3.37	**0.005**
PM between – PS within	−20509	−2.14	0.142
PS between – PM within	33895	3.54	**0.003**
PS between – PS within	−16462	−1.84	0.259
PM within – PS within	−50357	−5.24	**<0.001**

Table S10. Distance between the interacting lizards: linear mixed model.

Term	F	df	p
Encounter type	—	2	**0.039**
Sex	0.01	1	0.930
Location	0.46	2	0.634
Year	0.55	1	0.459
Body size (SVL)	0.49	1	0.484

Table S11. Distance between the interacting lizards: Tukey post-hoc contrasts.

Contrast	estimate	t.ratio	p
Between-species – PM within	13.08	2.59	**0.027**
Between-species – PS within	−4.85	−0.95	0.612
PM within – PS within	−17.93	−2.67	**0.022**

D. Intraspecific Signalling

Table S12. Conspicuousness of the lateral blue spot: full ANOVA for chromatic (dS) and luminance (dL) contrast.

Response	Term	df	Sum Sq	F	p
Chromatic (dS)	Species	1	—	—	**0.003**
	Sex	1	—	—	**0.026**
	Location	2	—	—	0.77
	Species × Sex	1	—	3.14	0.082
Luminance (dL)	Species	1	16.39	1.29	0.262
	Sex	1	83.93	6.61	**0.013**
	Location	2	14.34	0.56	0.572
	Species × Sex	1	19.51	1.54	0.221
	Residuals	48	609.46		

E. Anti-Predator Behaviour and Visibility

E.1. Flight Initiation Distance (FID)

Table S13. Flight initiation distance: overall ANOVA.

Term	F	df	p
Species	149.50	1	**<0.001**
Sex	1.18	1	0.279
Location	0.87	2	0.420
Time of day	7.25	1	**0.007**

E.2. Flight Distance (FD)

Table S14. Flight distance: full ANOVA.

Term	Sum Sq	df	F	p
Species	63608.4	1	40.26	**<0.001**
Sex	3423.4	1	2.17	0.142
Location	635.3	2	0.20	0.818
Species × Sex	6280.9	1	3.98	**0.047**
Species × Location	5147.9	2	1.63	0.197
Sex × Location	1310.8	2	0.41	0.661
Species × Sex × Location	4954.6	2	1.57	0.210
Time of day	1324.4	1	0.84	0.360

E.3. Hiding Duration (HD)

Table S15. Decision to hide: logistic regression, full coefficients (N = 451).

Term	coef	SE	z	p
Species (PS)	−0.915	0.596	−1.54	0.125
Sex (M)	−0.310	0.533	−0.58	0.560
Location (Pag)	0.107	0.583	0.18	0.855
Location (Sinj)	0.379	0.477	0.79	0.427
Species:Sex	1.206	0.780	1.55	0.122
Species:Loc(Pag)	1.101	0.817	1.35	0.178
Species:Loc(Sinj)	0.781	0.755	1.03	0.301
Sex:Loc(Pag)	0.127	0.753	0.17	0.866
Sex:Loc(Sinj)	−0.338	0.716	−0.47	0.637
Species:Sex:Loc(Pag)	—	—	—	**0.037**
Species:Sex:Loc(Sinj)	−0.154	1.049	−0.15	0.883
Time of day	−0.004	0.002	−2.67	**0.008**

Table S16. Time to emergence among hiders: Cox model (N = 143).

Term	HR	SE	z	p
Species (PS)	0.971	0.191	−0.15	0.877
Sex (M)	1.162	0.190	0.79	0.432
Location (Pag)	0.870	0.236	−0.59	0.557
Location (Sinj)	0.746	0.243	−1.20	0.228
Time of day	0.999	0.002	−0.40	0.688

E.4. Visibility to Predators

Table S17. Modelled visibility to predators: complete per-background ANOVA results for species, sex, and location across the lower-back (brown) and upper-back (green) patches, luminance and chromatic contrasts, and bird and snake visual models (significant p-values in bold).

Patch / contrast / predator	Background	Species F	Species p	Sex F	Sex p	Loc F	Loc p
Green luminance bird	Anthropogenic	9.50	**0.003**	5.08	**0.028**	2.21	0.120
	Branch	23.86	**<0.001**	0.97	0.329	4.72	**0.013**
	Stone	13.56	**<0.001**	5.65	**0.021**	4.95	**0.011**
	Leaf	17.00	**<0.001**	1.35	0.250	3.31	**0.044**
	Grass	15.16	**<0.001**	1.94	0.169	3.54	**0.036**
	Ground	27.76	**<0.001**	0.08	0.779	3.02	0.057
Green luminance snake	Anthropogenic	18.77	**<0.001**	4.59	**0.037**	3.95	**0.025**
	Branch	25.49	**<0.001**	1.36	0.249	4.44	**0.016**
	Stone	10.96	**0.002**	7.27	**0.009**	3.03	0.056
	Leaf	30.42	**<0.001**	0.81	0.372	4.82	**0.012**
	Grass	29.19	**<0.001**	1.31	0.257	5.45	**0.007**
	Ground	28.87	**<0.001**	0.08	0.781	2.84	0.067
Green chromatic bird	Anthropogenic	11.50	**0.001**	1.30	0.260	1.72	0.188
	Branch	9.39	**0.003**	2.14	0.149	1.32	0.275
	Stone	12.05	**0.001**	1.85	0.179	1.29	0.284
	Leaf	10.52	**0.002**	0.60	0.442	1.23	0.299
	Grass	9.72	**0.003**	2.83	0.098	1.45	0.243
	Ground	12.39	**<0.001**	0.48	0.492	1.55	0.222
Green chromatic snake	Anthropogenic	6.72	**0.012**	0.48	0.491	1.01	0.370
	Branch	6.72	**0.012**	0.51	0.480	1.01	0.372
	Stone	6.73	**0.012**	0.47	0.495	1.02	0.366
	Leaf	5.79	**0.020**	0.23	0.631	1.04	0.360
	Grass	6.00	**0.018**	0.29	0.592	1.04	0.361
	Ground	6.23	**0.016**	0.34	0.562	1.05	0.358
Brown luminance bird	Anthropogenic	4.68	**0.035**	1.66	0.203	1.37	0.264
	Branch	3.29	0.075	1.93	0.170	0.08	0.921
	Stone	6.98	**0.011**	1.93	0.170	1.22	0.304
	Leaf	6.13	**0.016**	2.82	0.099	1.42	0.249
	Grass	8.80	**0.004**	1.63	0.207	2.74	0.073
	Ground	13.68	**<0.001**	0.94	0.336	1.48	0.238
Brown luminance snake	Anthropogenic	4.97	**0.030**	1.80	0.185	1.42	0.250
	Branch	2.98	0.090	1.77	0.188	0.05	0.953
	Stone	7.24	**0.009**	2.15	0.149	1.31	0.277
	Leaf	6.00	**0.017**	2.83	0.098	1.39	0.257

Patch / contrast / predator	Background	Species F	Species p	Sex F	Sex p	Loc F	Loc p
	Grass	5.24	**0.026**	2.50	0.120	1.63	0.204
	Ground	11.79	**0.001**	0.49	0.488	2.17	0.124
Brown chromatic bird	Anthropogenic	0.27	0.603	4.34	**0.042**	2.25	0.115
	Branch	0.31	0.580	4.16	**0.046**	2.28	0.112
	Stone	0.24	0.626	4.43	**0.040**	2.25	0.115
	Leaf	0.22	0.639	5.80	**0.019**	1.69	0.195
	Grass	0.16	0.694	5.13	**0.028**	2.26	0.114
	Ground	0.00	0.992	3.13	0.082	2.91	0.063
Brown chromatic snake	Anthropogenic	0.02	0.885	4.09	**0.048**	1.91	0.158
	Branch	0.02	0.876	4.14	**0.047**	1.89	0.160
	Stone	0.01	0.909	4.14	**0.047**	1.92	0.157
	Leaf	0.01	0.936	4.45	**0.040**	1.75	0.183
	Grass	0.01	0.925	4.37	**0.041**	1.79	0.177
	Ground	0.01	0.935	4.13	**0.047**	1.87	0.164

Table S18. Modelled visibility to predators: complete Tukey-adjusted pairwise comparisons among locations (Knin, Pag, Sinj) for green-patch luminance contrast on backgrounds with a significant location effect, under bird and snake visual models. Estimates, standard errors (SE), t-values, and adjusted p-values are reported; significant p-values ($p < 0.05$) are shown in bold.

Background	Comparison	Estimate	SE	t	p
Bird predators					
	Knin – Pag	0.591	0.240	2.42	**0.049**
Branch	Knin – Sinj	-0.107	0.240	-0.45	0.896
	Pag – Sinj	-0.698	0.240	-2.86	**0.016**
	Knin – Pag	-0.745	0.260	-2.83	**0.018**
Stone	Knin – Sinj	-0.051	0.260	-0.20	0.979
	Pag – Sinj	0.694	0.260	2.64	**0.029**
	Knin – Pag	0.423	0.260	1.62	0.246
Leaf	Knin – Sinj	-0.242	0.260	-0.94	0.617
	Pag – Sinj	-0.665	0.260	-2.55	**0.036**
	Knin – Pag	0.440	0.260	1.70	0.216
Grass	Knin – Sinj	-0.243	0.260	-0.95	0.613
	Pag – Sinj	-0.683	0.260	-2.63	**0.029**
Snake predators					
	Knin – Pag	-0.600	0.225	-2.66	**0.027**
Anthropogenic	Knin – Sinj	-0.128	0.222	-0.57	0.835
	Pag – Sinj	0.472	0.222	2.12	0.095
	Knin – Pag	0.563	0.242	2.32	0.061

Background	Comparison	Estimate	SE	t	p
Branch	Knin – Sinj	-0.114	0.239	-0.48	0.882
	Pag – Sinj	-0.677	0.242	-2.79	**0.019**
	Knin – Pag	0.561	0.228	2.46	**0.045**
Leaf	Knin – Sinj	-0.088	0.225	-0.39	0.919
	Pag – Sinj	-0.649	0.225	-2.88	**0.015**
	Knin – Pag	0.583	0.220	2.66	**0.028**
Grass	Knin – Sinj	-0.076	0.217	-0.35	0.935
	Pag – Sinj	-0.659	0.217	-3.04	**0.010**

F. Dorsal Pattern Variation and Camouflage

F.1. Camouflage Effectiveness

Table S19. Composite camouflage score: full linear mixed-model ANOVA (Type III, Satterthwaite).

Term	NumDF	DenDF	F	p
Species (SPEC)	1	123	4.80	**0.030**
Sex	1	123	2.08	0.139
Location (LOC)	2	123	3.08	0.051
Background	5	611	55.14	**<0.001**
SPEC × Sex	1	123	1.28	0.260
SPEC × LOC	2	123	0.03	0.990
Sex × LOC	2	123	0.46	0.630
SPEC × Background	5	611	23.49	**<0.001**
Sex × Background	5	611	2.55	**0.043**
LOC × Background	10	611	1.92	**0.027**
SPEC × Sex × LOC	2	123	0.46	0.635
SPEC × Sex × Background	5	611	1.31	0.258
SPEC × LOC × Background	10	611	20.81	**<0.001**
Sex × LOC × Background	10	611	0.82	0.606
SPEC × Sex × LOC × Background	10	611	0.39	0.952

Table S20. Composite camouflage score: species post-hoc (*Podarcis melisellensis*, PM − *Podarcis siculus*, PS) for every Location × Background combination (Tukey-adjusted).

Location	Background	estimate (PM−PS)	t.ratio	p
Knin	Anthropogenic	0.014227	0.398	0.6914
Pag	Anthropogenic	-0.092927	-2.723	**0.0072**
Sinj	Anthropogenic	0.035614	0.992	0.3227
Knin	Complex	0.062527	1.748	0.0824
Pag	Complex	0.156521	4.587	**<.0001**
Sinj	Complex	0.055949	1.558	0.1211
Knin	Vegetation	-0.014601	-0.406	0.6853
Pag	Vegetation	0.157937	4.614	**<.0001**
Sinj	Vegetation	0.015497	0.430	0.6674
Knin	Stone	0.051785	1.447	0.1497
Pag	Stone	0.000368	0.011	0.9914
Sinj	Stone	0.028807	0.802	0.4236
Knin	Bark	0.081335	2.273	**0.0243**
Pag	Bark	0.076233	2.234	**0.0268**
Sinj	Bark	0.046208	1.287	0.1999
Knin	Ground	0.046041	1.287	0.1999
Pag	Ground	-0.025098	-0.735	0.4631
Sinj	Ground	0.055306	1.540	0.1254

F.2. Dorsal Pattern Variation

Table S21. Dorsal pattern: Random Forest 5-fold cross-validated balanced accuracy (ResNet50 deep features).

Grouping	Balanced accuracy ± SD	Chance
Species	0.897 ± 0.068	0.500
Sex	0.695 ± 0.083	0.500
Species × Sex	0.605 ± 0.043	0.250
Location	0.544 ± 0.053	0.333
Species × Location	0.515 ± 0.086	0.167
Sex × Location	0.361 ± 0.088	0.167
Species × Sex × Location	0.329 ± 0.082	0.083

Table S22. Dorsal pattern: PERMANOVA (Euclidean; 999 permutations).

Grouping	pseudo-F	R^2	p
Species	4.24	0.031	**0.001**
Sex	2.20	0.016	**0.001**
Location	1.99	0.029	**0.001**
Species × Sex	—	0.054	**0.001**
Species × Location	2.70	0.095	**0.001**
Sex × Location	—	0.061	**0.001**
Species × Sex × Location	1.89	0.144	**0.001**

Table S23. Dorsal pattern: PERMDISP (within-group multivariate dispersion).

Grouping	F	p
Species	1.90	0.181
Sex	1.32	0.262
Location	0.79	0.446
Species × Sex	2.31	0.085
Species × Location	—	0.506
Sex × Location	—	0.098
Species × Sex × Location	—	0.221

Table S24. Descriptive morphometrics (mean ± SD) of the laboratory cohort (N = 230) by species, sex, and location. SVL = snout–vent length; ILL = interlimb length; SMI = scaled mass index; ILL/SVL and Hind/Fore are the interlimb and hindlimb-to-forelimb shape ratios. n is the number of individuals per cell.

Species	Sex	Site	n	SVL (mm)	ILL (mm)	Mass (g)	Hindlimb (mm)	Forelimb (mm)	SMI	ILL/SVL	Hind/Fore
PM	F	Knin	18	51.62 ± 5.28	29.36 ± 3.79	2.62 ± 0.61	21.14 ± 1.57	15.58 ± 1.36	4.67 ± 0.83	0.57 ± 0.02	1.36 ± 0.05
PM	F	Pag	21	49.68 ± 2.74	27.95 ± 2.67	2.35 ± 0.38	19.48 ± 1.18	14.25 ± 0.67	4.73 ± 0.61	0.56 ± 0.03	1.37 ± 0.06
PM	F	Sinj	16	55.83 ± 4.20	32.19 ± 3.06	3.08 ± 0.71	22.05 ± 1.71	16.30 ± 0.82	4.14 ± 0.55	0.58 ± 0.02	1.35 ± 0.07
PM	M	Knin	19	57.35 ± 5.94	30.39 ± 3.07	4.08 ± 1.30	25.78 ± 2.75	18.52 ± 1.83	4.95 ± 0.70	0.53 ± 0.02	1.39 ± 0.06
PM	M	Pag	20	53.93 ± 2.56	28.53 ± 2.13	3.26 ± 0.63	22.70 ± 1.21	16.46 ± 0.59	4.94 ± 0.59	0.53 ± 0.03	1.38 ± 0.07
PM	M	Sinj	19	62.89 ± 2.94	33.73 ± 1.58	5.48 ± 0.75	27.93 ± 1.74	19.99 ± 0.91	5.00 ± 0.47	0.54 ± 0.02	1.40 ± 0.05
PS	F	Knin	19	65.57 ± 5.67	36.80 ± 4.17	5.34 ± 1.34	28.61 ± 2.18	20.58 ± 1.62	4.22 ± 0.72	0.56 ± 0.03	1.39 ± 0.04
PS	F	Pag	21	63.85 ± 5.12	36.64 ± 3.95	4.71 ± 1.11	27.53 ± 1.67	19.88 ± 1.29	4.06 ± 0.55	0.57 ± 0.03	1.39 ± 0.05
PS	F	Sinj	19	66.15 ± 7.09	38.33 ± 5.06	5.68 ± 1.88	28.29 ± 2.24	20.35 ± 1.52	4.22 ± 0.30	0.58 ± 0.02	1.39 ± 0.06
PS	M	Knin	19	75.70 ± 4.98	40.31 ± 2.83	10.15 ± 1.86	36.02 ± 2.39	25.56 ± 1.52	4.95 ± 0.52	0.53 ± 0.02	1.41 ± 0.04
PS	M	Pag	21	66.31 ± 5.75	35.56 ± 3.87	6.90 ± 1.96	31.61 ± 3.29	22.35 ± 1.82	5.16 ± 0.46	0.54 ± 0.02	1.41 ± 0.05
PS	M	Sinj	18	74.25 ± 5.58	40.37 ± 3.09	9.37 ± 2.25	35.17 ± 3.43	24.98 ± 2.03	4.82 ± 0.48	0.54 ± 0.03	1.41 ± 0.05

Table S25. Adjusted repeatability (R, one-way intraclass correlation of residuals after adjusting for trial, sex, and location) with cluster-bootstrap 95% confidence intervals (1000 resamples over individuals), per species and movement variable.

Species	Movement variable	R	95% CI lower	95% CI upper
PM	Angular velocity	0.631	0.504	0.731
PM	Distance moved	0.545	0.432	0.634
PM	Number of moving segments	0.363	0.233	0.476
PM	Movement duration	0.361	0.234	0.466
PS	Angular velocity	0.550	0.440	0.635
PS	Distance moved	0.545	0.432	0.629
PS	Number of moving segments	0.354	0.206	0.473
PS	Movement duration	0.427	0.265	0.544

Table S26. Sample sizes for the two field-derived datasets, by location, species and sex. (a) All individuals for which anti-predator behaviour was recorded in the field (flight initiation distance, flight distance and hiding duration): 226 in 2020 and 225 in 2021. (b) The subset for which just-noticeable-difference (JND) values were obtained, balanced by design at five males and five females of each species at each location; each of these individuals contributes 40 JND values (two predator visual models × two body patches × five backgrounds × two contrast types), and the species-specific models in Tables 4 and 5 are each fitted on the 30 individuals of that species.

	P. melisellensis		***P. siculus***		
Location	**M**	**F**	**M**	**F**	**Total**
(a) Field behavioural sample (N = 451)					
Knin	41	34	38	36	149
Pag	52	24	40	34	150
Sinj	38	52	31	31	152
Total	**131**	**110**	**109**	**101**	**451**
(b) Colouration (JND) subset (N = 60)					
Knin	5	5	5	5	20
Pag	5	5	5	5	20
Sinj	5	5	5	5	20
Total	**15**	**15**	**15**	**15**	**60**

8. Curriculum Vitae

Tomislav Gojak was born on May 12th 1994 in Zagreb, Croatia. He received his undergraduate degree in biology (univ. bacc. biol.) in 2017 and his master's degree in experimental biology (mag. biol. exp.) in 2020 at the Faculty of Science, University of Zagreb, with a master's thesis on sociability in captive Italian wall lizards (*Podarcis siculus*) from the islets of Pod Kopište and Pod Mrčaru. Since 2020 he has been an assistant at the Department of Biology, Faculty of Science, and since 2024 works at the Association Hyla, first as an expert associate and, from 2025, as a senior expert associate. His research addresses animal behaviour, ecophysiology and comparative ecology, with a growing emphasis on computational modelling and data-driven approaches to interspecific interactions such as syntopy, combining laboratory and field work with applied data analysis. He has participated in six national and international research projects, including the Croatian Science Foundation projects on dopamine regulation of competitive behaviour and on phenotypic plasticity in *Podarcis siculus*, and as project leader for further developing the citizen-science platform *Biologer*. He has completed two research visits abroad, at Masaryk University in Brno and the Nencki Institute of Experimental Biology in Warsaw. At the Faculty of Science he has contributed to teaching across six courses. He has co-authored eight peer-reviewed journal articles (one in press; listed below) and presented his research at six national and international conferences. He is fluent in Croatian and English.

Publications

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2. Perinović, M., Gojak, T., Glogoški, M., Pavin, L., Čižmek, H., & Lisičić, D. (2026). Population density and spatial–temporal niche use of ship rats and Italian wall lizards on a small Adriatic island. *Ecology and Evolution*, *16*(8), e74003.
3. Zadravec, M., Cesarec, R., Smutni, B., Zadravec, M., Gojak, T., Glogoški, M., & Lisičić, D. (2026). Predictors of body temperature in nose-horned viper (*Vipera ammodytes*) across different populations. *Animals*, *16*(8), 1239.
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7. Glogoški, M., Hocenski, K., Gojak, T., Blažević, S. A., Hranilović, D., & Lisičić, D. (2024). Behavioural traits for success: Comparison between two sympatric lacertid lizard species. *Animal Behaviour*, *218*, 263–273.

8. Pekár, S., Gajski, D., Mifková, T., Smolinský, R., Gojak, T., & Martišová, M. (2023). Natural diet of European green lizards, *Lacerta viridis* (Squamata: Lacertidae): A comparison of macroscopic and molecular identification methods. *Herpetologica*, *79*(3), 135–143.