Ecology and conservation of the Balkan chamois (*Rupicapra rupicapra balcanica*) in Greece

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PhD Thesis

Department of Biological Applications and Technology
University of Ioannina
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UNIVERSITY
OF IOANNINA

Οικολογία και Διατήρηση του Βαλκανικού Αγριόγιδου (*Rupicapra rupicapra balcanica*) στην Ελλάδα

Κωνσταντίνος Παπακώστας

Διδακτορική Διατριβή

Τμήμα Βιολογικών Εφαρμογών και Τεχνολογιών
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Artificial Intelligence (AI) declaration

During the creation of this work, I have used AI to aid me with light linguistic improvement suggestions (ChatGPT). Additionally, I have used AI to help me identify and tackle errors while running R code during data analysis.

FINO ALLA FINE…E OLTRE

Contents

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Abstract

The Balkan chamois (*Rupicapra rupicapra balcanica*) is an emblematic mountain ungulate and one of the seven subspecies of the Northern chamois (*R. rupicapra*). Greece marks the southernmost edge of its European distribution. Although national legislation protects the species and prohibits hunting since 1969, the subspecies maintains an Inadequate-Bad conservation status. Poaching, road development, and hunting of other game species drive the main threats, while livestock competition, tourism, mining projects, genetic isolation, and climate change add further pressure. Greece has approved an action plan for the species, but it is not yet implemented.

To contribute to this plan and strengthen conservation efforts, this thesis examines key ecological aspects of the Balkan chamois in Greece. It assessed seasonal range use and habitat selection in two mountains that differ in climatic conditions (dry/wet), analyzed diel and seasonal activity patterns, produced a national habitat suitability map, and quantified potential habitat loss and fragmentation driven by climate change and renewable energy development. It also synthesized current knowledge on home range and habitat selection for both Northern and Southern chamois.

On Mt. Olympus, we collected 1,182 chamois observations during four seasonal surveys in 2022 and 2023 and estimated population size. The annual range reached 103 km^2. The smallest range occurred in autumn during the rut, followed by summer, and the largest in winter. The species showed a Mediterranean range use pattern, which indicates that summer drought acts as the main ecological stressor. The population numbered roughly 430 individuals and showed an increasing trend, although fecundity remained low in 2022. Ecological Niche Factor Analysis (ENFA) revealed that chamois selected areas close to hiking trails throughout the year, likely due to habituation to hikers, and avoided mountain roads, which aligns with strategies that minimize poaching risk. It also selected rocky habitats and escape terrain, especially in spring and winter. These findings refine approaches for identifying escape terrain and mapping suitable habitat and support management measures that include road control, water provision in dry mountains, visitor regulation, anti-poaching actions, and expansion of hunting-free areas.

On Mt. Oiti, we recorded 652 chamois occurrences in 2023 across a study area of 156 km^2. Seasonal ranges and core areas showed limited variation and strong spatial overlap, which indicates minimal seasonal movement. Species Distribution Models identified 12.2 km^2 of suitable habitat, and 28% of this area lay outside the Natura 2000 network. Chamois used forests in all seasons and expanded their use of grasslands in summer and autumn. Human disturbance variables exerted the strongest influence on habitat suitability. The species consistently avoided areas near livestock pens, roads, and hunting grounds. Planned wind power stations would lead to 17% loss of the suitable habitat and would likely reduce the population's range, while the impact of proposed small hydroelectric units remains uncertain. These results highlight the need to restrict infrastructure and road construction in suitable habitat, expand protected areas and wildlife refuges, and regulate livestock pressure, all in line with the national action plan.

Although chamois are widely distributed across Europe and parts of Asia (ten subspecies), studies on their distribution and habitat selection account for less than 10% of the literature on the genus, and existing research disproportionately focuses on the Alpine chamois (*R. r. rupicapra*). We explored the chamois home range patterns and habitat selection drivers, trends in methodological data collection and analysis tools, and research gaps. We conducted a systematic search (PRISMA guideline) and a meta-analysis of the peer-reviewed, English-language articles that reported quantitative data on home range size or habitat selection, comprising 22 studies spanning 16 study

areas. Knowledge stemmed mainly (68% of studies) from the Alpine subspecies. Seven subspecies remain understudied (0-1 study each). Telemetry and field observations were the primary field methods in home range and habitat selection studies, respectively. Annual individual home ranges were small but varied greatly (0.04-4.94 km^2), depending on sex (larger in males), dispersal behavior (larger in migrating males), and season. Habitat selection analysis (24 factors tested; 452 cases) revealed that topography (elevation, slope, escape terrain) and human disturbance (hunting, infrastructure, hiking trails, livestock) influenced chamois habitat selection. Rocky, grassland and forest habitat use were season-dependent, and snow-covered areas were generally avoided. We highlight the need for further research on underrepresented and threatened subspecies, as well as on the chamois' responses to human disturbance and climatic variables, to better inform conservation management under global change.

We also performed the first assessment of the activity patterns of the Balkan chamois in Greece using camera traps, with a focus on potential differences between forested and open habitats. We deployed 49 camera traps across Pindos mountain range (2015-2020), targeting areas with high chamois presence. Thirty-nine cameras yielded usable data (6,152 camera days). We quantified Relative Abundance Index (RAI) and analyzed seasonal and diel activity patterns based on independent photographic events. Chamois showed a high RAI (43), with daily activity ranging from 9:00 to 21:00 and a peak at 11:00. Chamois used both forested and open areas, but we found no substantial differences in their activity patterns between the two. Nocturnal activity was generally low but increased during autumn, coinciding with the rutting season. We recommend a systematic camera trap deployment in future studies to evaluate activity overlap with sympatric species and the effects of human disturbance on chamois behavior.

Εκτενής Περίληψη στα Ελληνικά/Extensive Greek Summary

Γενική εισαγωγή

Το Βαλκανικό αγριόγιδο (*Rupicapra rupicapra balcanica*), είναι υποείδος του Βόρειου αγριόγιδου (*R. rupicapra*), και αποτελεί είδος σύμβολο των ελληνικών βουνών. Το Βαλκανικό αγριόγιδο έχει κατανομή σε 9 διαφορετικές χώρες της Βαλκανικής χερσονήσου (Ελλάδα, Κροατία, Βοσνία και Ερζεγοβίνη, Σερβία, Μαυροβούνιο, Βόρεια Μακεδονία, Κόσοβο, Αλβανία, και Βουλγαρία) και αριθμεί περίπου 9,000 άτομα συνολικά (Corlatti et al., 2022a). Στην Ελλάδα το πληθυσμιακό μέγεθος κυμαίνεται μεταξύ 1,330-1,765 ατόμων σε 30 διαφορετικούς πληθυσμούς (Papaioannou, 2021).

Το Βόρειο αγριόγιδο εμπεριέχεται στην κατηγορία Least Concern (LC) της IUCN, ενώ το βαλκανικό αγριόγιδο περιλαμβάνεται επιπλέον στα Παραρτήματα II και IV της οδηγίας 92/43 ΕΟΚ και στο Παράρτημα III της Σύμβασης της Βέρνης. Στην Ελλάδα κατατάσσεται στο Κόκκινο Βιβλίο των Απειλούμενων Ζώων ως Σχεδόν Απειλούμενο (NT). Είναι είδος προστατευόμενο και το κυνήγι του απαγορεύεται (ΝΔ 86/69) σε όλη τη χώρα. Η Κατάσταση Διατήρησης στην Ελλάδα το 2019 αξιολογήθηκε ως Μη ευνοϊκή (Unfavorable – Bad, U2) (Papaioannou, 2021).

Η βασική απειλή για το είδος στην Ελλάδα είναι η λαθροθηρία. Άλλες σημαντικές απειλές είναι η διάνοιξη και η χρήση οδικού δικτύου, η κτηνοτροφία σε σχέση με τον τρόπο και την ένταση εξάσκησής της υπό συγκεκριμένες προϋποθέσεις, ο κατακερματισμός της εξάπλωσης και η γενετική απομόνωση, η ενόχληση από το κυνήγι άλλων ειδών, οι τουριστικές δραστηριότητες και τα ορεινά σπορ, η εξόρυξη ορυκτών, και η κλιματική αλλαγή. Οι πληθυσμοί του αγριόγιδου που βρίσκονται στις συνοριακές ζώνες με τις γειτονικές χώρες των Βαλκανίων επηρεάζονται αρνητικά σε σημαντικό βαθμό και από παρεμβάσεις που προέρχονται από τις άλλες χώρες και από την έλλειψη διακρατικής συνεργασίας για τη διατήρηση του είδους (Papaioannou, 2021).

Το εθνικό σχέδιο δράσης για το είδος, το οποίο περιλαμβάνει μέτρα διατήρησης και προστασίας του είδους, έχει εγκριθεί χωρίς όμως να έχει υλοποιηθεί ακόμη (Papaioannou, 2021).

Η παρούσα διδακτορική διατριβή εξετάζει τα πρότυπα εποχικής διασποράς του αγριόγιδου στην Ελλάδα, τα πρότυπα δραστηριότητας, τις προτιμήσεις ενδιαιτημάτων, τις πιθανές επιπτώσεις της κλιματικής αλλαγής και των εγκαταστάσεων ανανεώσιμων πηγών ενέργειας στα κατάλληλα ενδιαιτήματα του είδους, καθώς και μια σύνοψη της υπάρχουσας επιστημονικής γνώσης για τη διασπορά και τις προτιμήσεις ενδιαιτήματος των αγριόγιδων.

Επομένως, η διατριβή περιλαμβάνει:

Το **Κεφάλαιο 1**, το οποίο παρέχει μια συνοπτική γενική περιγραφή του είδους και της κατάστασής του στην Ελλάδα.

Το **Κεφάλαιο 2**, το οποίο εξετάζει τα εποχικά πρότυπα διασποράς και προτίμησης ενδιαιτήματος στο Όρος Όλυμπος.

Το **Κεφάλαιο 3**, το οποίο εξετάζει τα εποχικά πρότυπα διασποράς και προτίμησης ενδιαιτήματος στο Όρος Οίτη, καθώς και τις πιθανές επιπτώσεις της εγκατάστασης ανανεώσιμων πηγών ενέργειας στο κατάλληλο ενδιαίτημα του είδους.

Το **Κεφάλαιο 4**, παρουσιάζει μια γενική σύνοψη της υπάρχουσας γνώσης για τη διασπορά και τις προτιμήσεις ενδιαιτήματος του είδους, σε παγκόσμιο επίπεδο.

Το **Κεφάλαιο 5**, εξετάζει τα μοτίβα συμπεριφοράς των αγριόγιδων στη Βορειοδυτική Ελλάδα με τη χρήση καμερών-παγίδων, καθώς και την πιθανή διαφορά στη δραστηριότητα μεταξύ δασωμένων και ανοιχτών περιοχών.

Τέλος, παρουσιάζεται μια γενική σύνοψη των ευρημάτων της διατριβής και προτείνονται μέτρα διατήρησης αλλά και προτάσεις για εκτεταμένη μελλοντική έρευνα του είδους στη χώρα.

Μεθοδολογία

Περιοχές μελέτης

Η περιοχή μελέτης του **Κεφαλαίου 2** αφορά το Όρος Όλυμπος (40°5'8"N, 22°21'31"E), με έκταση 248 km^2. Περιλαμβάνει το 86% του Εθνικού Πάρκου Ολύμπου, του πρώτου εθνικού πάρκου στην Ελλάδα, και είναι περιοχή Natura 2000. Είναι μια ορεινή περιοχή με υψόμετρο 297-2,918 μ. και 84% άνω των 1,000 μ. Το γεωλογικό υπόστρωμα αποτελείται κυρίως από ασβεστόλιθο (99%). Η ετήσια βροχόπτωση είναι 841 χιλιοστά, η θερμοκρασία κυμαίνεται από -13.5 °C έως 33.8 °C.
Η περιοχή μελέτης του **Κεφαλαίου 3** αφορά το Όρος Οίτη (38°49'43"N 22°17'19"E). Έχει έκταση 248 km^2 με υψόμετρο 92-2,152 μ. (81% άνω των 1,000 μ.). Το γεωλογικό υπόστρωμα αποτελείται κυρίως από ασβεστόλιθο (60%) και φλύσχη (32%). Η ετήσια βροχόπτωση είναι 854 χιλιοστά, και η θερμοκρασία κυμαίνεται μεταξύ -16.4 °C και 33.7 °C.
Η περιοχή μελέτης για το **Κεφάλαιο 5** περιλαμβάνει μέρος της Βόρειας Πίνδου, με έκταση 946 km^2. Στην περιοχή υπάρχουν πέντε περιοχές Natura 2000 και τέσσερα Καταφύγια Άγριας Ζωής (ΚΑΖ).

Μέθοδοι δειγματοληψίας

Στα Όρη Όλυμπος (**Κεφάλαιο 2**) και Οίτη (**Κεφάλαιο 3**), πραγματοποιήθηκε έρευνα πεδίου και τις τέσσερις εποχές του έτους (άνοιξη: 27/4-3/5; καλοκαίρι: 27/6-3/7; φθινόπωρο: 22/9-28/9; χειμώνας: 7/12-13/12), για τον εντοπισμό άμεσων (αγριόγιδα) και έμμεσων (κόπρανα, ίχνη) παρουσιών του είδους. Για την έρευνα χρησιμοποιήσαμε τηλεσκόπιο και κιάλια για τον εντοπισμό, καθώς και συσκευή GPS για την καταγραφή των παρουσιών. Στο Όρος Όλυμπος (2022-2023) πραγματοποιήσαμε έξι διαφορετικές διαδρομές συνολικού μήκους 70 χιλιομέτρων κάθε εποχή, ενώ στο Όρος Οίτη (2023) πέντε διαδρομές συνολικού μήκους 24 χιλιομέτρων.
Για το **Κεφάλαιο 5** χρησιμοποιήσαμε δεδομένα του Εργαστηρίου Διατήρησης της Βιοποικιλότητας, στο οποίο πραγματοποιήθηκε η παρούσα διδακτορική διατριβή. Χρησιμοποιήσαμε δεδομένα (φωτογραφίες) από κάμερες-παγίδες.

Ανάλυση δεδομένων

Εποχική διασπορά

Για τον υπολογισμό της έκτασης (σε km^2) της ετήσιας και εποχικής διασποράς του πληθυσμού των Βαλκανικών αγριόγιδων στα Όρη Όλυμπος (Κεφάλαιο 2) και Οίτη (Κεφάλαιο 3) χρησιμοποιήσαμε η μέθοδος Kernel Density Estimates (KDE) 95%, με το πακέτο "adehabitatHR" (Calenge, 2006; Worton, 1989) στο πρόγραμμα R (R Core Team, 2023). Για τον υπολογισμό χρησιμοποιήσαμε όλες τις παρουσίες από κάθε βουνό για την ετήσια διασπορά, και τις παρουσίες κάθε εποχής για την εποχική διασπορά.

Προτίμηση ενδιαιτήματος

Για το **Κεφάλαιο 2** (Όρος Όλυμπος) αξιολογήσαμε τις εποχικές προτιμήσεις ενδιαιτήματος του είδους, χρησιμοποιώντας την μέθοδο Ecological Niche Factor Analysis (ENFA).
Για την ανάλυση χρησιμοποιήσαμε εννέα περιβαλλοντικές μεταβλητές σε κλίμακα 25x25 m. Αρχικά, το υψόμετρο, τον Δείκτη Τραχύτητας Εδάφους (Terrain Ruggedness Index, TRI), και τον Δείκτη Τοπογραφικής Υγρασίας (Topographic Wetness Index, TWI) χρησιμοποιώντας το Ευρωπαϊκό Ψηφιακό Μοντέλο Εδάφους (Copernicus Land Monitoring Service, Version 3, 2021) και το πακέτο

“terra” (Hijmans et al., 2022). Στη συνέχεια χαρτογραφήσαμε τρεις βασικούς τύπους ενδιαιτημάτων στην περιοχή μελέτης: λιβάδια, δάση και βραχώδεις εκτάσεις. Χρησιμοποιήσαμε δορυφορικές εικόνες υψηλής ανάλυσης (Copernicus Open Access Hub, Sentinel-2, 2022) και ταξινομήσαμε τα ενδιαιτήματα στις τρεις κατηγορίες εκπαιδεύοντας τον αλγόριθμο του εργαλείου ταξινόμησης στο Γεωγραφικό Σύστημα Πληροφοριών (GIS) με 50 πολύγωνα ανά τύπο ενδιαιτήματος. Τέλος, υπολογίσαμε τρεις μεταβλητές απόστασης, οι οποίες αντιστοιχούν στις μικρότερες αποστάσεις των καταγραφών αγριόγιδων από: (α) καταφύγιο διαφυγής, (β) δρόμους (ασφαλτοστρωμένους και χωμάτινους) και (γ) μονοπάτια πεζοπορίας. Ορίσαμε ως καταφύγιο διαφυγής τα πολύγωνα που παρουσίαζαν κλίση μεγαλύτερη από 45° και εμβαδόν άνω των τεσσάρων κελιών (>2.500 m^2). Λάβαμε υπόψη το οδικό δίκτυο της περιοχής (138 km δρόμων) (δεδομένα από το Εργαστήριο Διατήρησης Βιοποικιλότητας που χρησιμοποιήθηκαν για τον εθνικό χάρτη “roadless”) (Kati et al., 2023b), καθώς και το δίκτυο μονοπατιών πεζοπορίας (305 km) (Hellaspath, 2022). Για όλους τους υπολογισμούς απόστασης χρησιμοποιήσαμε το πακέτο “distanceto” (Miller et al., 2019).

Η οικολογική θέση (niche) του είδους αποτελείται από δύο συνιστώσες στον οικολογικό χώρο: τη διαφορικότητα (marginality) και την εξειδίκευση (specialization). Η διαφορικότητα μετρά τον βαθμό διαφοροποίησης μεταξύ των μέσων περιβαλλοντικών συνθηκών στο ενδιαίτημα που χρησιμοποιείται και των διαθέσιμων συνθηκών στην περιοχή μελέτης. Η εξειδίκευση αποτυπώνει το εύρος της οικολογικής θέσης και αντικατοπτρίζει την ανοχή του είδους στις μεταβολές των περιβαλλοντικών συνθηκών.

Συμπεριλάβαμε όλες τις μεταβλητές στο μοντέλο (Spearman $|r| \leq 0.75$) και χρησιμοποιήσαμε όλες τις άμεσες και έμμεσες καταγραφές ανά εποχή ως σημεία παρουσίας (ενδιαιτήματα που χρησιμοποιήθηκαν), καθώς και ένα σύνολο 1,182 τυχαίων σημείων σε όλη την περιοχή μελέτης (διαθέσιμο ενδιαίτημα). Στη συνέχεια προσδιορίσαμε τον βαθμό στον οποίο κάθε μεταβλητή συνέβαλε στη διαφορικότητα και την εξειδίκευση μέσω της αντίστοιχης τιμής συμβολής στους άξονες της ανάλυσης. Η στατιστική σημαντικότητα ελέγχθηκε με τη διαδικασία τυχαιοποίησης Monte Carlo (1,000 επαναλήψεις). Για την ανάλυση χρησιμοποιήσαμε το πακέτο “adehabitatHS” (Calenge, 2011a).

Για το **Κεφάλαιο 3** (Όρος Οίτη), χρησιμοποιήσαμε μια περιβαλλοντική βάση δεδομένων δέκα μεταβλητών, σε κλίμακα 25 × 25 m, που σχετίζονται με το ανάγλυφο, τους κύριους τύπους βλάστησης και τους παράγοντες ανθρωπογενούς όχλησης. Υπολογίσαμε τρεις τοπογραφικές μεταβλητές (υψόμετρο, κλίση και τραχύτητα εδάφους) χρησιμοποιώντας Ψηφιακό Μοντέλο Εδάφους (DEM) ανάλυσης 25 m (Copernicus Land Monitoring Service, Version 3, 2021). Για τον υπολογισμό της κλίσης και της τραχύτητας χρησιμοποιήσαμε τη συνάρτηση “terrain” του πακέτου “terra” (Hijmans et al., 2022). Λάβαμε υπόψη τρεις κύριους τύπους βλάστησης σύμφωνα με την τυπολογία EUNIS (Davies et al., 2004): δάση (G1–G5), λιβάδια (E1, E2, E4, F2) και θάμνους (F5). Υπολογίσαμε επίσης τέσσερις μεταβλητές που σχετίζονται με ανθρωπογενή όχληση. Χρησιμοποιήσαμε το οδικό δίκτυο (263 km) (OSM, 2025) για να υπολογίσουμε την απόσταση από τον πλησιέστερο δρόμο (ασφαλτοστρωμένο ή χωμάτινο). Παράλληλα, χρησιμοποιήσαμε τη διαθέσιμη βάση δεδομένων των ποιμνιοστασίων (50 εγκαταστάσεις) (Iliopoulos et al., 2015) που παρείχε η τοπική Μονάδα Διαχείρισης του ΟΦΥΠΕΚΑ, καθώς και τα πολύγωνα των περιοχών απαγόρευσης θήρας (geodata.gov.gr), για να υπολογίσουμε τις αντίστοιχες αποστάσεις από αυτά τα στοιχεία.

Επιπλέον, χαρτογραφήσαμε το καταφύγιο διαφυγής ως απότομες (>45°) και εκτεταμένες (≥2.500 m^2) κλίσεις (Papakostas et al., 2025b) και υπολογίσαμε την απόσταση των καταγραφών από αυτές.

Οι υπολογισμοί απόστασης πραγματοποιήθηκαν στο ArcGIS Pro (έκδοση 3.1.0) με το εργαλείο "Distance Accumulation".

Για τις προτιμήσεις ενδιαιτήματος του είδους υπολογίσαμε τη μέση τιμή των περιβαλλοντικών μεταβλητών στα σημεία παρουσίας του αγριόγιδου για κάθε εποχή και για όλο το έτος (ενδιαίτημα που χρησιμοποιήθηκε). Στη συνέχεια δημιουργήσαμε 652 τυχαία σημεία (αναλογία 1:1 μεταξύ παρουσιών και τυχαίων σημείων) στο ArcGIS Pro και εκτιμήσαμε τις μέσες τιμές των μεταβλητών σε αυτά τα σημεία εντός της περιοχής μελέτης (διαθέσιμο ενδιαίτημα). Χρησιμοποιώντας τον μη παραμετρικό έλεγχο Kruskal–Wallis H, εξετάσαμε αν οι περιβαλλοντικές μεταβλητές διέφεραν σημαντικά μεταξύ των τεσσάρων εποχών. Επιπλέον, συγκρίναμε τις ετήσιες περιβαλλοντικές μεταβλητές μεταξύ των σημείων παρουσίας και των τυχαίων σημείων (ενδιαίτημα που χρησιμοποιήθηκε έναντι διαθέσιμου ενδιαιτήματος) μέσω του ελέγχου Mann–Whitney U ($p < 0.05$).

Καταλληλότητα ενδιαιτήματος

Για το **Κεφάλαιο 3**, χρησιμοποιήσαμε το πακέτο "sdm" στο πρόγραμμα R (Naimi & Araújo, 2016) για τη μοντελοποίηση του κατάλληλου ενδιαιτήματος του είδους και την παραγωγή του αντίστοιχου χάρτη καταλληλότητας ενδιαιτήματος. Αρχικά, αξιολογήσαμε τη πολυσυγγραμμικότητα μεταξύ των μεταβλητών χρησιμοποιώντας τον Συντελεστή Διόγκωσης Διασποράς (Variance Inflation Factor, VIF) μέσω της συνάρτησης "vifstep" (όριο < 3) (Dormann et al., 2013; Zuur et al., 2010). Ο VIF βασίζεται στο τετράγωνο του συντελεστή πολλαπλής συσχέτισης (R^2) που προκύπτει από την παλινδρόμηση μιας μεταβλητής πρόγνωσης έναντι όλων των υπολοίπων, αποτελώντας ακριβέστερη μέθοδο σε σχέση με τη συσχέτιση Pearson (Naimi & Araújo, 2016).

Δεδομένου ότι δεν είχαμε πραγματικά δεδομένα απουσίας, προσαρμόσαμε τη βάση δεδομένων παρουσιών σε πλαίσιο μοντέλων παρουσίας-ψευδοαπουσίας δημιουργώντας ψευδοαπουσίες. Για τον σκοπό αυτό χρησιμοποιήσαμε τη μέθοδο Random Forest (RF) και αναλογία 1:1 μεταξύ παρουσιών και ψευδοαπουσιών, όπως προτείνεται για εφαρμογές RF στην οικολογία (Barbet-Massin et al., 2012). Χρησιμοποιήσαμε δύο δείκτες αξιολόγησης της επίδοσης του μοντέλου: την AUC και το TSS. Η AUC αξιολογεί την ικανότητα του μοντέλου να διακρίνει μεταξύ παρουσιών και απουσιών, με τιμές από 0-0.5 (τυχαία πρόβλεψη) έως 1 (τέλεια πρόβλεψη), και αποτελεί ευρέως χρησιμοποιούμενο δείκτη σε οικολογικές μελέτες (Fielding & Bell, 1997). Το TSS λαμβάνει υπόψη τόσο την ευαισθησία (true positive rate) όσο και την ειδικότητα (true negative rate), με τιμές από −1 έως 1, όπου το 1 υποδηλώνει τέλεια συμφωνία και τιμές ≤ 0 απόδοση μη καλύτερη της τυχαιότητας (Allouche et al., 2006).

Στη συνέχεια, συνδυάσαμε τα αποτελέσματα όλων των μοντέλων RF δημιουργώντας μια ensemble πρόβλεψη, η οποία ενσωματώνει πολλαπλά μοντέλα, αυξάνοντας την αξιοπιστία των τελικών εκτιμήσεων καταλληλότητας (Araújo & New, 2007). Αξιολογήσαμε τις πιο σημαντικές μεταβλητές χρησιμοποιώντας δύο δείκτες: τη συσχέτιση Pearson και την AUC. Η συσχέτιση Pearson αναδεικνύει τη γραμμική συμβολή κάθε μεταβλητής στο μοντέλο (Franklin, 2010), ενώ η AUC καταγράφει τη συνολική επίδραση των μεταβλητών (Lobo et al., 2008), περιλαμβάνοντας μη γραμμικές επιδράσεις και αλληλεπιδράσεις. Υιοθετήσαμε αυτή τη διπλή προσέγγιση ώστε να επιτύχουμε πιο ολοκληρωμένη αξιολόγηση της σημασίας των προβλεπτικών μεταβλητών, συνδυάζοντας συμπληρωματικές πτυχές της επίδρασής τους.

Τέλος, ορίσαμε ως κατάλληλες τις περιοχές με προβλεπόμενες τιμές καταλληλότητας υψηλότερες από τον μέσο όρο των τιμών καταλληλότητας των δεδομένων εκπαίδευσης (Liu et al., 2013).

Πρότυπα δραστηριότητας

Για το **Κεφάλαιο 5**, ταυτοποιήσαμε χειροκίνητα όλες τις εικόνες από τις κάμερες παγίδες (camera traps) χρησιμοποιώντας το λογισμικό ανοικτής πρόσβασης Wild.ID (Rovero & Zimmermann, 2016). Στη συνέχεια εξαγάγαμε ολόκληρη τη βάση δεδομένων, συμπεριλαμβανομένων της ημερομηνίας, της ώρας και του είδους, για την ανάλυση.

Για την ποσοτικοποίηση της δραστηριότητας των ειδών, υπολογίσαμε τον αριθμό των ανεξάρτητων καταγραφών ανά είδος, εφαρμόζοντας κατώφλι 15 λεπτών ώστε να αποφύγουμε την καταμέτρηση επαναλαμβανόμενων εικόνων του ίδιου ατόμου (Rovero & Zimmermann, 2016). Υπολογίσαμε τις ημέρες λειτουργίας κάθε φωτογραφικής παγίδας ως το σύνολο των περιόδων των 24 ωρών μεταξύ της εγκατάστασης και της συλλογής, ή έως την τελευταία καταγραφή στην περίπτωση που η κάρτα μνήμης είχε γεμίσει πριν τη συλλογή. Στη συνέχεια υπολογίσαμε τον δείκτη RAI (Relative Abundance Index) διαιρώντας τον αριθμό των γεγονότων με τον αριθμό των ημερών δειγματοληψίας και πολλαπλασιάζοντας το αποτέλεσμα επί 100.

Λόγω του σχεδιασμού της δειγματοληψίας μας, που επικεντρωνόταν στη δραστηριότητα του αγριόγιδου, αποκλείσαμε τις αναλύσεις επικάλυψης δραστηριότητας με άλλα είδη, καθώς τα αποτελέσματα ήταν στατιστικά μη σημαντικά. Για να εξετάσουμε τις διαφορές μεταξύ δασωμένων και ανοικτών ενδιαιτημάτων, ταξινομήσαμε ως δασικές τις κατηγορίες G της τυπολογίας EUNIS και ως ανοικτές τις κατηγορίες E και F. Για μια ισορροπημένη σύγκριση μεταξύ τύπων ενδιαιτήματος, διατηρήσαμε όλες τις κάμερες που λειτουργούσαν σε ανοικτές περιοχές και επιλέξαμε ίσο αριθμό δασικών καμερών με τον υψηλότερο αριθμό ανεξάρτητων γεγονότων αγριόγιδου.

Για τη διερεύνηση των διαφορών στη δραστηριότητα μεταξύ ενδιαιτημάτων και εποχών, χρησιμοποιήσαμε το πακέτο "overlap" για την παραγωγή καμπυλών εκτίμησης Kernel (kernel density estimation) (Meredith & Ridout, 2014), και υπολογίσαμε τον συντελεστή επικάλυψης Δ_4 για κάθε ζεύγος (Ridout & Linkie, 2009). Ο συντελεστής Δ κυμαίνεται από μηδέν, που υποδηλώνει απουσία επικάλυψης, έως ένα, που υποδηλώνει πλήρη επικάλυψη, και θεωρείται υψηλός όταν $\Delta > 0.75$, μέτριος όταν $0.50 < \Delta < 0.75$ και χαμηλός όταν $\Delta < 0.50$ (Monterroso et al., 2014). Υπολογίσαμε τα 95% διαστήματα εμπιστοσύνης του συντελεστή επικάλυψης με 10,000 επαναληπτικές δειγματοληψίες bootstrap (Rovero & Zimmermann, 2016).

Σύνοψη έρευνας και meta-analysis

Για το **Κεφάλαιο 4**, πραγματοποιήσαμε αναζήτηση βιβλιογραφίας στη βάση Scopus έως και την 1η Μαρτίου 2025, χρησιμοποιώντας συγκεκριμένους όρους αναζήτησης στον τίτλο, την περίληψη και τις λέξεις-κλειδιά: «chamois», «isard», «habitat selection», «habitat use», «habitat preferences», «ecological niche», «home range», «distribution» και «core area». Η αναζήτηση περιορίστηκε σε άρθρα δημοσιευμένα σε αγγλική γλώσσα και δημοσιευμένα σε επιστημονικά περιοδικά, και απέδωσε συνολικά 193 άρθρα.

Μετά τον έλεγχο των τίτλων και των περιλήψεων, αποκλείσαμε 161 άρθρα που δεν ήταν σχετιζόμενα με το είδος ή το αντικείμενο της μελέτης. Επιπλέον αποκλείσαμε τέσσερις μελέτες που δεν παρείχαν δεδομένα για το μέσο ή ατομικό μέγεθος home range, έξι περιγραφικές μελέτες που δεν περιλάμβαναν στατιστική επεξεργασία δεδομένων και μία μελέτη για την οποία δεν υπήρχε πρόσβαση στο πλήρες κείμενο. Αυτή η αρχική διαλογή απέδωσε 21 άρθρα.

Αφού επιλέξαμε τις μελέτες αυτές, εξετάσαμε επίσης τις βιβλιογραφικές τους αναφορές και εντοπίσαμε μία επιπλέον σχετική μελέτη που δεν εμφανίστηκε στην αναζήτηση στη Scopus. Το τελικό σύνολο δεδομένων αποτελείτο από 22 μελέτες: οκτώ αφορούσαν την περιοχή home range, έντεκα την επιλογή ή χρήση ενδιαιτήματος, και τρεις εξέταζαν και τα δύο αντικείμενα.

Χρησιμοποιήσαμε περιγραφική στατιστική για να διερευνήσουμε τα κενά γνώσης και τις ερευνητικές τάσεις διαχρονικά, αξιοποιώντας το σύνολο των μελετών. Εστιάσαμε στα διαφορετικά είδη και υποείδη αγριόγιδου που έχουν μελετηθεί, καθώς και στις τεχνικές συλλογής και ανάλυσης δεδομένων. Χαρτογραφήσαμε τις περιοχές μελέτης που περιλαμβάνονται στη βάση δεδομένων δημιουργώντας χάρτη στο ArcGIS Pro (έκδοση 3.2.2).

Χρησιμοποιώντας το σύνολο δεδομένων home range, συνοψίσαμε τα μεγέθη home range ξεχωριστά για αρσενικά και θηλυκά, βάσει των τιμών που αναφέρονται σε κάθε μελέτη. Για κάθε φύλο υπολογίσαμε περιγραφικά στατιστικά, όπως τη μέση τιμή και την τυπική απόκλιση, καθώς και τις ελάχιστες και μέγιστες τιμές, ώστε να αποτυπώσουμε τη μεταβλητότητα στο μέγεθος της περιοχής home range. Επιπλέον, αναφέραμε τα αποτελέσματα από τρεις μελέτες που διαχώρισαν τα αρσενικά σε «μόνιμους κατοίκους» (resident: αρσενικά που κατοικούν σε μικρές και σταθερές home range) και «μετακινούμενα» (migrant: αρσενικά που μετακινούνται μεταξύ εποχικών περιοχών) (Lovari et al., 2006; Nesti et al., 2010; Unterthiner et al., 2012).

Χρησιμοποιώντας το σύνολο δεδομένων επιλογής ενδιαιτήματος, αναλύσαμε τα αποτελέσματα των μελετών τύπου GLM μέσω μετα-ανάλυσης τυχαίων επιδράσεων για κάθε παράγοντα, χρησιμοποιώντας το πακέτο “metafor” στο πρόγραμμα R (Viechtbauer, 2010). Συνδυάσαμε τα μεγέθη επίδρασης (β) μεταξύ των μελετών, σταθμισμένα με βάση την αντίστροφη διακύμανσή τους ($1/SE^2$). Ποσοτικοποιήσαμε την ετερογένεια μεταξύ των μελετών μέσω των δεικτών τ^2 (διακύμανση πραγματικών επιδράσεων) και I^2 (βαθμός επικάλυψης διαστημάτων εμπιστοσύνης). Για να αξιολογήσουμε τη συμβολή των μεσολαβητών, υπολογίσαμε το R^2 ως εκτίμηση του ποσοστού ετερογένειας που εξηγείται (Borenstein et al., 2021; Nakagawa et al., 2023; Schwarzer, 2022).

Για τη διερεύνηση της συμφραζόμενης μεταβλητότητας στην επιλογή ενδιαιτήματος, εκτελέσαμε μεικτές μετα-παλινδρομήσεις (mixed-effects meta-regressions) για όλους τους παράγοντες με σημαντική συνδυασμένη επίδραση, ενσωματώνοντας ως μεσολαβητές την εποχή (ετήσια, άνοιξη, καλοκαίρι, φθινόπωρο, χειμώνας) και τη μέθοδο ανάλυσης (π.χ. GLM). Συμπεριλάβαμε μεσολαβητές μόνο όταν υπήρχαν επαρκή δεδομένα σε κάθε κατηγορία για τον αντίστοιχο παράγοντα. Ως κατηγορία αναφοράς ορίσαμε την «ετήσια» εποχή και τη μέθοδο «GLM». Έτσι, οι σταθεροί όροι (intercepts) αντιπροσωπεύουν τις εκτιμώμενες επιδράσεις υπό αυτές τις βασικές συνθήκες. Χρησιμοποιήσαμε το Study ID ως τυχαία επίδραση για να ληφθεί υπόψη η ύπαρξη πολλαπλών εκτιμήσεων από την ίδια μελέτη. Δημιουργήσαμε διαγράμματα χρησιμοποιώντας το πακέτο “ggplot2” (Wickham, 2016).

Για την αξιολόγηση της επιλογής ενδιαιτήματος στις μελέτες που χρησιμοποίησαν ENFA, εξαγάγαμε τις τιμές διαφορικότητας (marginality) για όλες τις περιβαλλοντικές μεταβλητές που εξετάστηκαν σε κάθε μελέτη. Ο άξονας διαφορικότητας ποσοτικοποιεί τον βαθμό στον οποίο το χρησιμοποιούμενο ενδιαίτημα διαφέρει από τις μέσες διαθέσιμες συνθήκες, με θετικές και αρνητικές τιμές να υποδηλώνουν επιλογή και αποφυγή αντίστοιχα (Hirzel et al., 2002). Κατατάξαμε κάθε παράγοντα με βάση την κατεύθυνση της διαφορικότητας (M): θετική (επιλογή), αρνητική (αποφυγή) ή ουδέτερη. Θεωρήσαμε ουδέτερες τις τιμές $M \leq 0.2$.

Για τη σύνοψη των αποτελεσμάτων εφαρμόσαμε προσέγγιση vote-counting (Borenstein et al., 2021). Για κάθε παράγοντα υπολογίσαμε τον αριθμό θετικών, αρνητικών και ουδέτερων αποτελεσμάτων σε όλες τις μελέτες ENFA, και στη συνέχεια υπολογίσαμε έναν απλό δείκτη επιλογής (θετικά – αρνητικά) ώστε να αποτυπωθούν οι γενικοί τάσεις. Η μέθοδος αυτή επιτρέπει τη σύγκριση των προτιμήσεων ενδιαιτήματος σε επίπεδο παραγόντων μεταξύ μελετών, χωρίς να

απαιτούνται τα ακατέργαστα αποτελέσματα των μοντέλων, τα οποία δεν είναι πάντα διαθέσιμα στις ENFA αναλύσεις.
Οι δείκτες selection ratios εκτιμούν την ισχύ επιλογής σε σχέση με τη διαθεσιμότητα ενδιαιτήματος, αλλά συχνά στερούνται εκτιμήσεων διακύμανσης ή συνεπούς κλίμακας μεταξύ μελετών (Manly et al., 2002). Για κάθε παράγοντα κατατάξαμε την κατεύθυνση επιλογής ως Θετική (επιλέγεται), Αρνητική (αποφεύγεται) ή Ουδέτερη (καμία σημαντική διαφορά μεταξύ χρήσης και διαθεσιμότητας ή τιμή δείκτη ≈ 1). Στη συνέχεια εφαρμόσαμε την ίδια προσέγγιση vote-counting καταγράφοντας τα θετικά, αρνητικά και ουδέτερα αποτελέσματα σε όλες τις μελέτες selection ratios. Τέλος, υπολογίσαμε έναν δείκτη επιλογής (θετικά – αρνητικά) για κάθε παράγοντα ώστε να αποτιμήσουμε τη συνέπεια και την ισχύ της επίδρασής του μεταξύ μελετών. Μία μελέτη που αξιολόγησε την επιλογή ενδιαιτήματος με βασική περιγραφική στατιστική αποκλείστηκε από την ανάλυση.

Αποτελέσματα-Συζήτηση

Κεφάλαιο 2

Η ετήσια έκταση διασποράς του πληθυσμού στο Όρος Όλυμπος καλύπτει μια έκταση 103 km^2. Αυτή η έκταση είναι μεγαλύτερη σε σχέση με άλλα ελληνικά βουνά, όπως το Όρος Τύμφη (Kati et al., 2020) και το Όρος Γκιώνα (Papaioannou et al., 2015), υποδεικνύοντας μεγάλη έκταση κατάλληλων ενδιαιτημάτων σε συνδυασμό με χαμηλή όχληση στο Όρος Όλυμπος.
Ένα βασικό εύρημα για την οικολογία των αγριόγιδων στο Όρος Όλυμπος είναι το εποχικό μοτίβο διασποράς του πληθυσμού, καθώς βρήκαμε πως η εποχή με τη μικρότερη έκταση διασποράς ήταν το φθινόπωρο, ακολουθούμενο από το καλοκαίρι, την άνοιξη και τέλος το χειμώνα. Στο τυπικό «Ηπειρωτικό» μοτίβο για τα αγριόγιδα στην Ευρώπη είναι γνωστό ότι ο χειμώνας είναι η εποχή με τη μικρότερη έκταση διασποράς, λόγω δύσκολων καιρικών συνθηκών που περιορίζουν την μετακίνηση και τα αποθέματα τροφής (Corlatti et al., 2023; Crampe et al., 2007; García-González et al., 1992; Nesti et al., 2010). Αντίθετα, στον Όλυμπο η θερμή εποχή του έτους φέρεται να είναι η κύρια περίοδος στρες για τα αγριόγιδα, ακολουθώντας ένα «Μεσογειακό» μοτίβο εποχικής κατανομής, το οποίο έχει παρατηρηθεί επίσης στο Όρος Γκιώνα (Papaioannou et al., 2015). Το «Μεσογειακό» εποχικό μοτίβο υποδηλώνει ότι το καλοκαίρι αποτελεί την περίοδο στρες· τα ζώα μετακινούνται σε ψυχρότερα μικροενδιαιτήματα σε μεγαλύτερα υψόμετρα, κοντά σε υπολείμματα χιονιού ή σε βόρειες πλαγιές, αναζητώντας φρέσκους, εύγευστους και υψηλής ποιότητας τροφικούς πόρους, με αποτέλεσμα να παρουσιάζουν περιορισμένη θερινή κατανομή. Πιστεύουμε ότι και άλλοι πληθυσμοί αγριόγιδου ενδέχεται να μεταβάλουν το εποχικό τους εύρος από «Ηπειρωτικό» σε «Μεσογειακό», με τους πληθυσμούς που ζουν ήδη σε μεσογειακά περιβάλλοντα να είναι οι πιθανότεροι να υιοθετήσουν αυτό το πρότυπο λόγω της κλιματικής αλλαγής.
Το μοντέλο μας έδειξε ξεκάθαρα ότι τα αγριόγιδα προτιμούσαν περιοχές κοντά στα μονοπάτια πεζοπορίας καθ' όλη τη διάρκεια του έτους. Αξιοσημείωτο είναι ότι αυτή είναι η πρώτη φορά που καταγράφεται τόσο ισχυρή προτίμηση των αγριόγιδων για μονοπάτια πεζοπορίας, δεδομένου ότι η πεζοπορία συνήθως έχει αρνητικές επιπτώσεις στην άγρια πανίδα (Peters et al., 2023). Ωστόσο, σε ορισμένες περιπτώσεις έχει αναφερθεί ότι τα αγριόγιδα αυξάνουν την ανοχή τους σε ανθρώπινες δραστηριότητες, μειώνοντας τη συμπεριφορά επαγρύπνησης σε περιοχές με υψηλά επίπεδα τουρισμού φύσης (Schuttler et al., 2017).
Στην περίπτωση του Ολύμπου, η θήρα απαγορεύεται, ωστόσο έχουν καταγραφεί περιστατικά λαθροθηρίας. Αποδίδουμε την προτίμηση για την εγγύτητα στα μονοπάτια πεζοπορίας στον αποτρεπτικό ρόλο της παρουσίας των πεζοπόρων στη λαθροθηρία. Τα μονοπάτια φαίνεται να προσφέρουν έμμεση προστασία από τη λαθροθηρία-που θεωρείται η σημαντικότερη απειλή για

το είδος (Papaioannou, 2021)-ενώ ενδέχεται να μειώνουν και το ενεργειακό κόστος μετακίνησης σε δύσβατα εδάφη.

Διαπιστώσαμε επίσης, ότι τα αγριόγιδα απέφευγαν σταθερά τους δρόμους στον Όλυμπο, εκτός από τη χειμερινή περίοδο. Το ίδιο πρότυπο έχει αναφερθεί και στο όρος Τύμφη, όπου το είδος συγκεντρώνεται στα πιο απομακρυσμένα σημεία του βουνού, μακριά από δρόμους και χωριά, για να αποφύγει τη λαθροθηρία και την ανθρώπινη όχληση (Kati et al., 2020). Στον Όλυμπο, κατά τη χειμερινή περίοδο, τα αγριόγιδα δε χρειάζεται να αποφεύγουν το οδικό δίκτυο, καθώς οι περισσότερες δασικές οδοί στα ανώτερα υψόμετρα είναι απροσπέλαστες λόγω χιονοκάλυψης.

Κεφάλαιο 3

Για το **Κεφάλαιο 3**, βρήκαμε ότι τα αγριόγιδα τροποποιούν ελάχιστα το εποχικό εύρος κατανομής, καθώς και οι τέσσερις εποχές είχαν σχετικά σταθερό μέγεθος έκτασης. Το είδος στην Οίτη φαίνεται να μην ακολουθεί κανένα από τα δύο εποχικά πρότυπα κατανομής που έχουν αναφερθεί στην Ευρώπη και την Ελλάδα, ούτε να αντιμετωπίζει σημαντικό κλιματικό στρες. Πιθανή αιτία αυτού αποτελεί το ότι τα ζώα κατοικούν σε δασωμένες περιοχές καθ' όλη τη διάρκεια του έτους, επωφελούμενα από την εκτεταμένη δασική κάλυψη, η οποία διευκολύνει τη θερμορύθμιση και προσφέρει καταφύγιο από τις ακραίες θερμοκρασίες, ενώ παράλληλα παρέχει και τροφικούς πόρους (Anderwald et al., 2024). Επιπλέον, ωφελούνται από τις ήπιες χειμερινές συνθήκες και τη μόνιμη διαθεσιμότητα νερού σε ρέματα και υδάτινα σώματα καθ' όλη τη διάρκεια του έτους.

Όπως και στο **Κεφάλαιο 2**, βρήκαμε ότι τα αγριόγιδα στην Οίτη αποφεύγουν την ανθρώπινη όχληση, προτιμώντας περιοχές μακριά από δρόμους, κτηνοτροφικές στάνες και περιοχές που επιτρέπεται το κυνήγι.

Η ανάλυσή μας έδειξε ότι τα προτεινόμενα σχέδια εγκατάστασης αιολικών σταθμών παρουσιάζουν σημαντική επικάλυψη με τα πλέον κατάλληλα ενδιαιτήματα του αγριόγιδου στην Οίτη. Η απώλεια ενδιαιτήματος αποτελεί μείζονα απειλή για το βαλκανικό αγριόγιδο σε όλη την εξάπλωσή του (Corlatti et al., 2022c). Τοποθετημένα σε λιβάδια υψηλού υψομέτρου (1,600–2,128 m), τα έργα αναμένεται να επιφέρουν σοβαρές πιέσεις στον τοπικό πληθυσμό, κυρίως μέσω της μείωσης των βοσκήσιμων εκτάσεων και της συνολικής απώλειας και κατακερματισμού του ενδιαιτήματος. Το είδος ενδέχεται να μετατοπίσει την κατανομή του μακριά από τις ανεμογεννήτριες, πιθανώς βρίσκοντας καταφύγιο στις πλέον δυσπρόσιτες δασικές ζώνες, δεδομένης της υψηλής του ευαισθησίας στην ανθρώπινη όχληση και των αρνητικών επιπτώσεων των ανεμογεννητριών που έχουν καταγραφεί για άλλα δασόβια μηρυκαστικά (Schöll & Nopp-Mayr, 2021).

Ο αντίκτυπος των υποδομών αιολικής ενέργειας υπερβαίνει την απώλεια ενδιαιτήματος μέσα στα επενδυτικά πολύγωνα (2,1 km^2), όπου οι ανεμογεννήτριες θα εγκατασταθούν σε τσιμεντένιες βάσεις. Το πραγματικό αποτύπωμα της χρήσης γης είναι μεγαλύτερο, καθώς συμπεριλαμβάνονται οι απαιτούμενες συνοδευτικές υποδομές (γραμμές μεταφοράς και πυλώνες ηλεκτρισμού, κτίρια λειτουργίας, καθώς και νέοι ή διαπλατυσμένοι δρόμοι πρόσβασης). Η αποψίλωση της βλάστησης κατά μήκος των δρόμων πρόσβασης θα επηρεάσει άμεσα τα δασικά ενδιαιτήματα του αγριόγιδου. Καμία από τις εννέα μικρές υδροηλεκτρικές εγκαταστάσεις που σχεδιάζονται δεν εμπίπτει σε κατάλληλα ενδιαιτήματα του αγριόγιδου. Η επίδρασή τους φαίνεται μικρή, ωστόσο παραμένει αβέβαιη. Δεν είναι γνωστό εάν οι εγκαταστάσεις θα επηρεάσουν τη διαθεσιμότητα νερού για την άγρια πανίδα στα ορεινά ρέματα και υδάτινα σώματα, ούτε το εύρος της κατάληψης γης που θα επιφέρει η ανάπτυξη οδικού δικτύου και των συνοδευτικών υποδομών.

Κεφάλαιο 4

Η σύνθεση όλων των μελετών για το **Κεφάλαιο 4** έδειξε ότι η διαθέσιμη γνώση προερχόταν κυρίως (68% των μελετών) από το αλπικό υποείδος αγριόγιδου (*R. r. rupicapra*). Επτά υποείδη παραμένουν ελάχιστα μελετημένα (0–1 μελέτη το καθένα). Η τηλεμετρία και οι παρατηρήσεις πεδίου αποτέλεσαν τις βασικές μεθόδους συλλογής δεδομένων για τις μελέτες home range και επιλογής ενδιαιτήματος, αντίστοιχα. Οι ετήσιες ατομικές home range ήταν μικρές αλλά με μεγάλη διακύμανση (0.04–4.94 km^2), επηρεαζόμενες από το φύλο (μεγαλύτερες στα αρσενικά), τη μεταναστευτική συμπεριφορά (μεγαλύτερες στα μετακινούμενα αρσενικά) και την εποχή.

Η ανάλυση επιλογής ενδιαιτήματος (24 παράγοντες, 452 περιπτώσεις) έδειξε ότι το ανάγλυφο (υψόμετρο, κλίση, καταφύγιο διαφυγής) και η ανθρωπογενής όχληση (θήρα, υποδομές, μονοπάτια πεζοπορίας, κτηνοτροφία) επηρέαζαν την επιλογή ενδιαιτήματος των αγριόγιδων. Η χρήση βραχωδών, λιβαδικών και δασικών ενδιαιτημάτων ήταν εξαρτώμενη από την εποχή, ενώ οι χιονοσκεπείς περιοχές αποφεύγονταν γενικά.

Κεφάλαιο 5

Συνολικά 39 κάμερες (16 σε ανοικτές περιοχές και 23 σε δάση) κατέγραψαν 6,152 ημέρες λειτουργίας (μέσος όρος ανά θέση 158±139), κατανεμημένες σε όλους τους μήνες του έτους (μέσος όρος ανά μήνα 513±121). Καταγράψαμε 6,173 ανεξάρτητα γεγονότα, εκ των οποίων 3,259 αφορούσαν άγρια θηλαστικά. Εντοπίσαμε 12 είδη άγριων θηλαστικών, με το αγριόγιδο να συγκεντρώνει τα περισσότερα γεγονότα (2,645), ακολουθούμενο από τον ευρωπαϊκό λαγό *Lepus europaeus* (175) και τον αγριόχοιρο *Sus scrofa* (117).

Λαμβάνοντας υπόψη ολόκληρο το σύνολο δεδομένων και τους δύο τύπους ενδιαιτήματος, η άνοιξη και το καλοκαίρι εμφάνισαν τη μεγαλύτερη επικάλυψη δραστηριότητας ($Δ_4$=0.93, CI: 0.89–0.95), ενώ η μικρότερη παρατηρήθηκε μεταξύ καλοκαιριού και φθινοπώρου ($Δ_4$=0.74, CI: 0.71–0.78). Το αγριόγιδο παρουσίασε αιχμή ημερήσιας δραστηριότητας γύρω στις 11:00, με γενικό εύρος δραστηριότητας από τις 9:00 έως τις 21:00 καθ' όλη τη διάρκεια του έτους. Τόσο στα δάση όσο και στις ανοικτές περιοχές, η δραστηριότητα κορυφωνόταν γύρω στις 11:00, ενώ το συνολικό μοτίβο ήταν σχετικά παρόμοιο ($Δ_4$=0.88, CI: 0.85–0.90).

Δεν παρατηρήσαμε ένα σαφές διμορφικό ημερήσιο μοτίβο, όπως έχει αναφερθεί για το αγριόγιδο (Darmon et al., 2014; Mason et al., 2014b) και άλλα ορεινά μηρυκαστικά (Li et al., 2020), ούτε μονοκορυφικό μοτίβο (Šprem et al., 2015). Αντιθέτως, τα μοτίβα δραστηριότητας παρουσίασαν εποχική διαφοροποίηση και συχνά εμφανίζονταν πολυτροπικά, όπως έχει αναφερθεί και σε άλλους πληθυσμούς (Brivio et al., 2016; Kavčić et al., 2021b).

Το φθινόπωρο, το αγριόγιδο εμφάνιζε επίσης υψηλή επικάλυψη δραστηριότητας μεταξύ δασωμένων και ανοικτών περιοχών ($Δ_4$=0.92, CI=0.89–0.95). Το μοτίβο αυτό ήταν έντονα πολυτροπικό, με τις δασωμένες περιοχές να δείχνουν κορυφώσεις γύρω στις 9:00 και 15:00, ενώ οι ανοικτές περιοχές γύρω στις 9:00.

Το φθινόπωρο το πολυτροπικό μοτίβο δραστηριότητας και η σημαντικά αυξημένη νυχτερινή δραστηριότητα σε σχέση με το υπόλοιπο έτος ενδέχεται να σχετίζονται με την περίοδο του ζευγαρώματος. Αν και η νυχτερινή δραστηριότητα έχει αναφερθεί καθ' όλη τη διάρκεια του έτους (Carnevali et al., 2016), συχνά εντείνεται κατά τη διάρκεια της αναπαραγωγικής περιόδου (Grignolio et al., 2018), ένα μοτίβο που ενδέχεται να αντανακλούν και τα δικά μας αποτελέσματα. Η νυχτερινή δραστηριότητα μπορεί επίσης να αυξηθεί ως απόκριση στη θερμότητα (Thel et al., 2024), αν και δεν παρατηρήσαμε τέτοια συμπεριφορά κατά τους θερμότερους μήνες.

Προτεινόμενα μέτρα διατήρησης

Η παρούσα διδακτορική διατριβή εμπλούτισε την επιστημονική γνώση για το Βαλκανικό αγριόγιδο στην Ελλάδα, στηρίζοντας εμπεριστατωμένα τα προτεινόμενα μέτρα διατήρησης που ήδη υπάρχουν στο Εθνικό Σχέδιο Δράσης για το είδος (Papaioannou, 2021).

Επομένως, για την αποτελεσματική προστασία και διατήρηση του είδους προτείνουμε:

- **Διατήρηση και βελτίωση ενδιαιτημάτων**

  ▪Παραγωγικές δραστηριότητες: i) Σύνταξη Σχεδίου Δράσης της αλληλεπίδρασης πληθυσμών αγριόγιδου και κτηνοτροφικών ζώων όπου αυτά συνυπάρχουν, ii) Σύνταξη οδηγιών καθορισμού ανώτερου επιπέδου φέρουσας ικανότητας για τα κτηνοτροφικά ζώα στα ενδιαιτήματα του αγριόγιδου σε συσχέτιση με την εξασφάλιση της βιωσιμότητας των τοπικών πληθυσμών του αγριόγιδου.

  ▪ Οδικό δίκτυο: i) Εφαρμογή περιορισμού της χρήσης υφιστάμενων δασικών και ορεινών δρόμων (σε εποχιακή ή ετήσια βάση) εντός ή κοντά στα κρίσιμα ενδιαιτήματα του είδους, ii) Σχέδιο δράσης για την διατήρηση περιοχών άνευ δρόμων που επικαλύπτονται με ενδιαιτήματα του είδους.

  ▪Δραστηριότητες αναψυχής: Σχέδιο Δράσης για τις δραστηριότητες αναψυχής (τουρισμός και υπαίθριες δραστηριότητες, κυνήγι άλλων ειδών άγριας πανίδας) στα ενδιαιτήματα του είδους και κυρίως στα κρίσιμα ενδιαιτήματα.

  ▪Εξασφάλιση πρόσβασης σε νερό: Δημιουργία θέσεων παροχής ύδατος σε επιλεγμένα μέρη για τον κάθε πληθυσμό του είδους.

- **Διατήρηση και επέκταση της ζώνης εξάπλωσης και περιορισμός του κατακερματισμού**

  ▪Διατήρηση της υφιστάμενης εξάπλωσης και ενίσχυση της επικοινωνίας μεταξύ των επιμέρους πληθυσμών, καθώς και της εγκατάστασης νέων πληθυσμών με φυσικό τρόπο: i) Παραγωγή χάρτη καταλληλόλητας του ενδιαιτήματος σε εθνική κλίμακα με μοντελοποίηση των κύριων παραμέτρων των οικολογικών απαιτήσεων του είδους στην ηπειρωτική Ελλάδα, ii) Σχέδιο Δράσης για την εξασφάλιση ικανοποιητικής και ορθά κατανεμημένης έκτασης με περιοριστικούς όρους στην εξάσκηση της δραστηριότητας του κυνηγίου σε σχέση με την εξάπλωση του είδους, iii) Σχέδιο Δράσης αναφορικά με την εκπόνηση μεγάλων κατασκευαστικών έργων στο εύρος κατανομής του είδους.

  ▪Ενδυνάμωση των υφιστάμενων πληθυσμών και εγκατάσταση νέων πληθυσμών με τεχνητό τρόπο: i) Εγκατάσταση νέων πληθυσμών με τεχνητή μεταφορά ατόμων από άλλους εύρωστους πληθυσμούς του είδους, ii) Ενδυνάμωση πολύ μικρών και απομονωμένων πληθυσμών με τεχνητή μεταφορά περιορισμένου αριθμού ατόμων από άλλους πληθυσμούς.

- **Πληθυσμιακή διατήρηση και βελτίωση**

  ▪Καθορισμός φέρουσας ικανότητας: Εκπόνηση μελέτης καθορισμού της φέρουσας ικανότητας σε κάθε γεωγραφική περιοχή όπου υπάρχει πληθυσμός του είδους θα προσδιοριστεί κατά πόσο οι διαθέσιμοι λιβαδικοί τύποι επαρκούν για τον πληθυσμό του αγριόγιδου και των ανταγωνιστών του (αγελάδες κ.λ.π.) λαμβάνοντας υπόψη τη βοσκοϊκανότητα των λιβαδικών τύπων και τη βοσκοφόρτωση τόσο από αγροτικά όσο και από άγρια χορτοφάγα ζώα.

  ▪Επόπτευση-φύλαξη: i) Επόπτευση και παρακολούθηση της χωρικής και χρονικής παρουσίας μέρους των πληθυσμών του είδους με τη βοήθεια κολάρων με δορυφορικούς πομπούς, ii) Δημιουργία και ενεργοποίηση αποτελεσματικών δομών εποπτείας- φύλαξης, iii) Εκπόνηση μελέτης και εφαρμογή Σχεδίου φύλαξης για την παράνομη θήρα για κάθε πληθυσμό ή ομάδα πληθυσμών αγριόγιδου, iv) Διενέργεια περιπολιών στις παραμεθόριες περιοχές διασυνοριακών πληθυσμών του είδους, με σκοπό την αποτροπή κρουσμάτων λαθροθηρίας από λαθροθήρες των γειτονικών χωρών, v) Πιλοτική εφαρμογή μηχανισμών πρόληψης και καταστολής περιβαλλοντικών παρανομιών (λαθροθηρία).

▪Διατήρηση γενετικής ευρωστίας: i) Καταγραφή της γενετικής ταυτότητας και της ποικιλομορφίας του κάθε πληθυσμού του είδους ή επιλεκτικά τουλάχιστον ενός πληθυσμού στην κάθε μία από τις έξι (6) κύριες ομάδες πληθυσμών, ii) Ταυτοποίηση του γενετικού προφίλ του πληθυσμού στην Ροδόπη (Δάσος Φρακτού) και συσχέτιση αυτού με εκείνο άλλων πληθυσμών του ιδίου ή διαφορετικών υποειδών του Βόρειου αγριόγιδου (π.χ. *R. r. rupicapra* και *R. r. carpatica*), iii) Ταυτοποίηση του γενετικού προφίλ και των ιδιαιτεροτήτων του πληθυσμού του είδους στο όρος Όλυμπος.

▪Ασθένειες και τραυματισμοί, σχέσεις με θηρευτές: i) Σύνταξη Σχεδίου καταγραφής ασθενειών του είδους, ii) Ενέργειες διάγνωσης και αποσαφήνισης της υφιστάμενης ασθένειας με εμφανή συμπτώματα στο δέρμα- τρίχωμα των ατόμων του είδους, η οποία έχει εντοπιστεί στην χαράδρα του Αώου στον πληθυσμό του όρους Τύμφη, iii) Σύνταξη Σχεδίου άμεσης παρέμβασης σε περίπτωση εντοπισμού τραυματισμένων ή άρρωστων ή νεκρών ατόμων του είδους, iv) Μελέτη διερεύνησης σχέσεων μεταξύ αγριόγιδου και λύκου.

- **Θεσμικό πλαίσιο (Νομοθεσία και πολιτική)**

  ▪Αποσαφήνιση υφιστάμενης νομοθεσίας και προτάσεις βελτίωσης: i) Σύνταξη έκθεσης αναφορικά με την υφιστάμενη νομοθεσία για το είδος και προτάσεις βελτίωσης αυτής, ii) Σύνταξη έκθεσης αναφορικά με τη χρήση ευρημάτων γενετικού υλικού (DNA) σε περιπτώσεις παράνομης θήρευσης, iii) Σύνταξη έκθεσης για το ηλεκτρονικό έγκλημα. Διασαφήνιση του καθεστώτος που διέπει το ηλεκτρονικό έγκλημα, iv) Διατύπωση οδηγιών για την αποφυγή αρνητικών επιπτώσεων στο αγριόγιδο εξαιτίας ειδικών τροποποιήσεων στη ετήσια ρύθμιση της θήρας λόγω της αύξησης του αγριόχοιρου.

Chapter 1. General Introduction

The Balkan chamois

General Information

The Balkan chamois (*Rupicapra rupicapra balcanica*) represents one of the seven subspecies of the Northern chamois in Europe and occupies the southernmost part of its distribution. Approximately 9,000 individuals live across nine Balkan countries: Greece, Croatia, Bosnia and Herzegovina, Serbia, Montenegro, North Macedonia, Kosovo, Albania, and Bulgaria (Corlatti et al., 2022a). Across its range, the subspecies faces several major threats that include the absence of coordinated cross-border management, competition with livestock, interbreeding with Alpine chamois (*R. r. rupicapra*), habitat loss, and poaching (Corlatti et al., 2022c).

The European Union lists the Balkan chamois in Annexes II and IV of the Habitats and Species Directive. In Greece, its national conservation status is U2 (Anderwald et al., 2021a), and the Greek National Red Data Book classifies it as Near Threatened (Legakis & Maragou, 2009). Greek legislation fully protects the subspecies, and hunting has remained banned nationwide since 1969 (Law 86/69). A great part (73,5%) of the Balkan chamois range in Greece overlaps with Natura 2000 sites, either Sites of Community Importance or Special Protection Areas.

The Greek Ministry of Environment launched species monitoring in 2014 for taxa listed in Annex 17 of Directive 92/43 EU (EEA 2019), which includes the Balkan chamois. The National Action Plan for the subspecies has been completed, but not yet implemented (Papaioannou, 2021).

Distribution and population status in Greece

Fig. 1.1 Distribution range of the Balkan chamois in Greece according to IUCN (Anderwald et al., 2021a)

The Balkan chamois population in Greece includes approximately 1,300 to 1,800 individuals that live in 30 subpopulations, with an increasing national trend (Anderwald et al., 2021a; Papaioannou, 2021). The IUCN range of the species in Greece covers 4,664.5 km^2 (**Fig. 1.1**) (Anderwald et al., 2021a).

Main threats in Greece

The three most important threats for the Balkan chamois in Greece are poaching, road infrastructure, and disturbance from hunting of other species (Papaioannou, 2021). Other threats are competition with livestock/overgrazing, tourism and mountain sports, climate change, mining, genetic isolation, and lack of cross border coordination (Papaioannou, 2021). **Table 1.1** summarizes the main threats affecting the Balkan chamois in Greece and their assessment based on the results of this PhD thesis.

Table 1.1 Threat types of the Balkan chamois in Greece across study areas, indicating presence (+) or absence (−) of each threat in the study area, together with the overall impact of each threat on the Balkan chamois as inferred from the results of this PhD thesis

Threat	Olympus	Oiti	Pindos	Impact
Poaching	+	+	+	NA
Infrastructure	+	+	+	Negative
Hunting of other species	-	+	+	Negative
Livestock	+	+	+	Negative
Tourism	+	-	+	Positive
Climate change	+	-	-	NA
Mining	-	+	-	NA
Genetic isolation	+	-	-	NA
Lack of cross-border coordination	-	-	+	NA

NA: Not Assessed

PhD thesis outline

Chapter 1

Presents a general introduction to the Balkan chamois in Greece.

Chapter 2

Investigates the seasonal home range and habitat selection of the Balkan chamois on Mt. Olympus. We attempted to: (a) delineate the seasonal and annual range and the respective core areas of the Balkan chamois on Mt. Olympus, (b) estimate its population size and demography, (c) explore the environmental, and (d) human-disturbance factors that drive its seasonal habitat selection process, and finally (e) interpret our findings under a climate change and conservation perspective.

Chapter 3

Investigates the seasonal home range and habitat selection of the Balkan chamois on Mt. Oiti, while also evaluating the potential impact of the renewable energy infrastructure. We aimed to: (a) explore the annual and seasonal ranges, including core areas frequently used by the population (b) pinpoint the key factors shaping suitable habitat and deliver a habitat suitability map, (c) explore the habitat preferences of the species, and (d) assess the impact of planned renewable energy infrastructure on chamois habitat.

Chapter 4

Aimed to provide a systematic overview and meta-analysis of the chamois' home range size and habitat selection, with the objectives of evaluating existing knowledge, identifying critical gaps, highlighting key environmental factors influencing the species' ecology, and offering guidance for future research and conservation efforts. We address the following questions: (a) How well are different chamois species and subspecies studied regarding their home range and habitat selection? (b) What are the research trends concerning the methodological tools used for data collection and analysis of chamois habitat use over the last four decades? (c) What are the home range and core area patterns of the species? (d) What are the primary factors shaping the habitat selection of the species according to different methodological analyses?

Chapter 5

Aimed to i) provide a camera trap-based assessment of activity patterns of the Balkan chamois in Greece and ii) test whether chamois exhibited different activity patterns between forested and open habitats.

Chapter 2. Seasonal distribution pattern and habitat selection of the Balkan chamois on Olympus mountain: Summer heat, hikers, roads

Published in *Journal for Nature Conservation*

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Abstract

The Balkan chamois (*Rupicapra rupicapra balcanica*) has a bad conservation status in Greece, and a national action plan will be implemented by the Ministry of Environment. We explored the seasonal distribution pattern and ecological preferences of the species on Mt. Olympus by collecting 1,182 observations of chamois occurrences across four seasonal surveys (2022-2023), and we estimated its population size (2022). The annual range of the species reached 103 km^2 (Kernel Density Estimator). We recorded the smallest seasonal range during autumn (rutting season), then in summer, and the largest in winter. The species followed the Mediterranean seasonal range use pattern, implying that summer is the stress period due to drought. The population size was c. 430 individuals, showing an increasing trend, but the fecundity rate was low in 2022. The Ecological Niche Factor Analysis (ENFA) showed that chamois preferred areas near hiking trails throughout the year, likely being habituated with visitors, while avoiding motorized roads, as adopted behaviors of poaching risk minimization. It also favored rocky areas and proximity to escape terrains during spring and winter. This work provides new methodological insights for habitat mapping and escape terrain definition (slope steepness and extent) and supports the suggested measures of the national action plan for implementing a roadless and road control policy, securing water availability in arid mountains, implementing a management plan for tourists, abating poaching and enlarging the hunting banning zone.

Keywords

Conservation; global warming; habitat selection; Mediterranean mountains; *Rupicapra rupicapra balcanica*; tourism.

Introduction

Mountain ungulates show adaptations to live on mountains, often acting as charismatic flagship species, but they occupy only 5% of Europe, mostly inhabiting protected areas (Linnell et al., 2020). Their role in the ecosystem is crucial: they serve as prey for large carnivores and carrion for scavengers, and they shape vegetation composition and soil properties, affecting a cascade of associated vertebrate and invertebrate species (Linnell et al., 2020). They are mostly threatened by habitat loss stemming from land use change and land artificialization, but also by harvesting, human disturbance, and climatic variations, which can affect their movement ecology, demographics, and foraging behavior (Lovari et al., 2020; Malpeli et al., 2024).

A good knowledge base of the ecological requirements of mountain ungulates and a deep understanding of the habitat selection process are prerequisites to predicting their distribution at a fine scale and informing conservation management decisions (Guisan et al., 2013). Habitat selection is a complex ecological process that involves a continuous trade-off between selecting habitats that maximize fitness through access to foraging and breeding resources while minimizing environmental stresses and anthropogenic risks (Northrup et al., 2022). Understanding such a process is particularly important for protected or threatened species subject to human pressures, as it informs conservation actions necessary for their survival and population recovery. Habitat selection is also a critical component in addressing applied ecological issues, such as predicting the effects of climate change and land-use changes on wildlife populations (Sohl, 2014).

This paper concerns the Balkan chamois, the southernmost subspecies of the Northern chamois (*Rupicapra rupicapra*) in Europe, protected under the European legislation (listed in Annexes II, IV of the Habitat Directive 92/43/EEC). It has an Unfavorable-Inadequate status (U1) at the alpine and continental zones and an Inadequate-Bad (U2) status in the Mediterranean zone, attributed mainly to the respective bad status of the national population in Greece (EIONET, 2019). The Balkan chamois forms small and often isolated populations across nine countries (less than 10,000 individuals) in the Balkan Peninsula and six discrete population blocks, including 30 subpopulations in Greece (1,500 individuals) (Anderwald et al., 2021a; Rezić et al., 2022). The species endorses a rotating seasonal moving pattern. It leaves the forested zone occupied in winter and gradually moves to higher altitudes in spring as the snow recedes. It inhabits the mountainous grasslands above the tree line during summer and autumn, while favoring proximity with screes and steep slopes used as escape terrains for protection (Corlatti et al., 2022b).

The conservation of the species is currently a national priority in Greece, with an approved national action plan anticipated for implementation soon (Papaioannou, 2021). According to the action plan, the area of suitable chamois habitats covers 7,409 km^2 (5.6% of Greece), but chamois occupies only one-fourth of it (1.5% of Greece), while the habitat quality is still unknown. The species is subject to a suite of anthropogenic pressures. According to the national action plan, poaching, the construction of new roads, and human disturbance through hunting act synergistically and stand at the top of the list. Other pressures include competition with livestock in the mountainous pastures, tourism, mining, genetic isolation, and global warming (Papaioannou, 2021). Some of the pressures, such as poaching, hunting disturbance and competition with livestock are common with the Bulgarian's action plan, which additionally considers as threat feral dogs and hybridization with other subspecies (Avramov & Valchev, 2010). The impact of tourism and of global warming on the species in Greece worths investigation. The presence of hikers and recreational activities can adversely affect wildlife in multiple ways (Wolf et al., 2019), such as disturbing natural behaviors, increased stress and habitat displacement. As the species inhabits high-elevation environments, it is particularly vulnerable to climatic variations that are expected to result in substantial habitat loss in the future (Salas et al., 2018; Sony et al., 2018). Climate change can further impact chamois populations by altering their distribution and reducing the availability of suitable habitats , by decreasing the body mass and survival rate in young chamois (Chirichella et al., 2021; Masoero et al., 2024), and by increasing the intraspecific conflicts due to heightened competition for limited resources (Fattorini et al., 2023).

Our work focused on the Balkan chamois population on Mt. Olympus, the oldest National Park of Greece (1938) that hosts the second largest population of the country (30% of the overall population), recently found to be a genetically differentiated population from the other five main population blocks occurring in the country (Papaioannou et al., 2019). In this paper, we attempted to: (a) delineate the seasonal and annual range and the respective core areas of the Balkan chamois on Mt. Olympus, (b) estimate its population size and demography, (c) explore the environmental, and (d) human-disturbance factors that drive its seasonal habitat selection process, and finally (e) interpret our findings under a climate change and conservation perspective. Besides increasing the knowledge base on the species ecology, we aimed to provide further evidence guiding the implementation of the action plan of the species at a local and national scale and hence contribute to the improvement of the Balkan chamois status at a European scale.

Materials and methods

Study area

The study area is located on Mount Olympus in central Greece (40°5'8"N, 22°21'31"E), covering an area of 248 km^2. It includes 86% of Olympus National Park's extent (**Fig. 2.1**). It was the first national park in the country and is currently a Natura 2000 site (GR 1250001) managed by the Natural Environment and Climate Change Agency (Management Unit of Olympus National Park). It is a mountainous area, from 297 m to 2,918 m, with an average altitude of 1,650 m and 84% of its extent above 1,000 m. The geological bedrock consists mainly of limestones (99%), inhibiting water retention and rendering the mountain arid, without permanent water sources above 1,100 m. The climate is Mediterranean at lower altitudes and temperate to intermediate to higher ones, with snow covering areas above 2,000 m from late October to late May (Strid, 1980). The annual precipitation is 841 mm. The temperature ranges from -13.5 °C (average of minimum values: January) to 33.8 °C (average of maximum values: July) (Data from Agios Dimitrios Meteorological Station, 881 m: 2020-2022). Four major vegetation zones were encountered (Strid, 1980): (a) evergreen–sclerophyllous Mediterranean scrub (300–600 m), (b) mixed beech and montane coniferous forests (700–1,500 m), (c) cool temperate coniferous forests (1,500–2,500 m) and (d) alpine meadows (2,500–2,918 m). Mt. Olympus hosts a rich flora and fauna, including chamois natural predators such as the grey wolf (*Canis lupus*), the brown bear (*Ursus arctos*), the red fox (*Vulpes vulpes*), and the golden eagle (*Aquila chrysaetos*) (Bousbouras et al., 2022). Besides the Balkan chamois, other ungulate species that inhabit lower altitudes are the roe deer (*Capreolus capreolus*) and the wild boar (*Sus scrofa*). Mountainous tourism, including nine mountain refugees, is the main human activity in the area (hiking, mountaineering, climbing, trail running). Hunting and

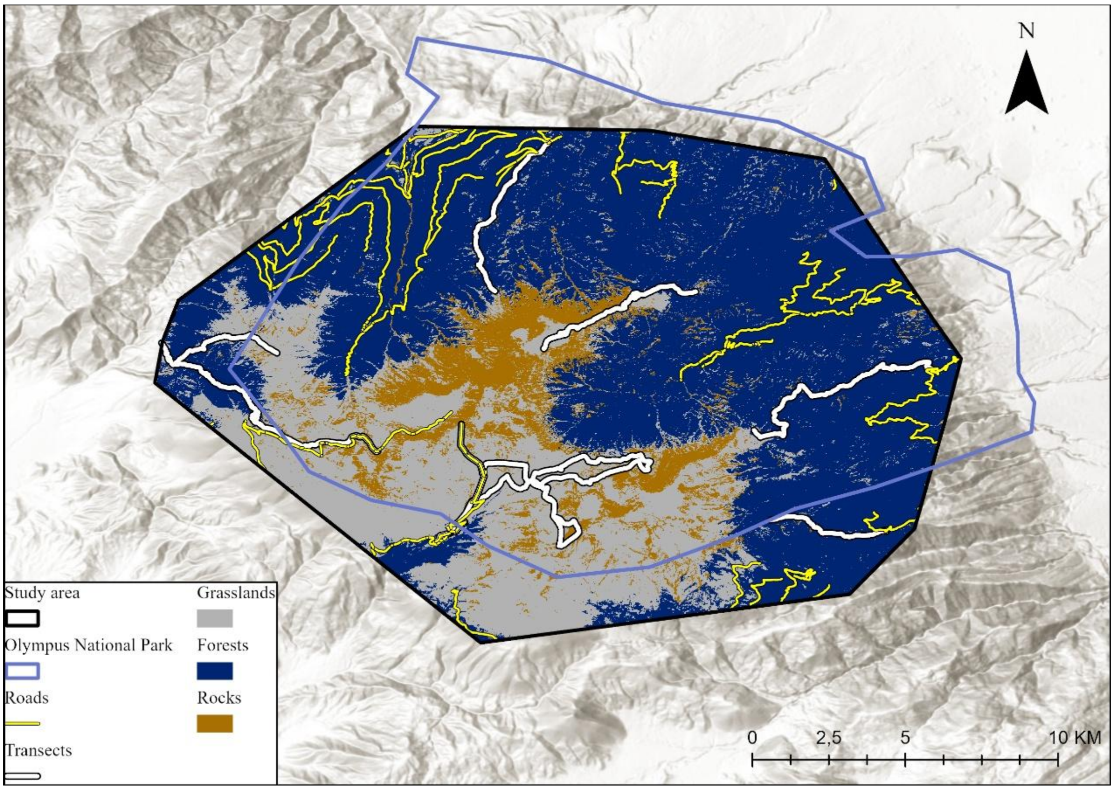


Fig. 2.1 Study area: Survey transects (2022) in the study area on Mt. Olympus across the main vegetation types

livestock breeding (cattle) are allowed only in a small part of the study area outside the National Park.

Chamois surveys

We considered four seasons according to chamois biology (Pepin et al., 1992): spring (including parturition period, 10/03–09/06), summer (warm period, 10/06–09/09), autumn (rutting period, 10/09–09/12), and winter (cold period, 10/12–09/03). We conducted six survey transects, totaling 70 km per season, in conjunction with a set of vantage points along them to represent the main habitat types and the elevation gradient (**Fig. 2.1**). We used binoculars and a telescope to collect observations, and a GPS device to georeference them, while noting the habitat type of the observation occurrence. The dataset included direct (animals) and indirect (pellets, tracks) observations. Considering the level of visibility (absence of trees) across the survey transects, the estimated area scanned was 50 km^2 (20% of the study area) (**Fig. 2A.1**).

To update the chamois population size estimation, we counted animals during the rutting period for five consecutive days in October 2022, using the "pointage flash method" (Houssin et al., 1994). We noted the date, time, coordinates, number of animals, and sex and age composition for each group: kids (<1 year), yearlings (between 1–2 years), adult females (>2 years), and adult males (>2 years) (Catusse, 1996). Duplicate observations of groups with the same composition in nearby localities as first observed were excluded from the dataset.

Environmental variables

The environmental dataset consisted of nine variables. We computed three topographic variables at a grid scale of 30x30 m: elevation, Terrain Ruggedness Index (TRI), and Topographic Wetness Index (TWI), using the European Digital Elevation Model (Copernicus Land Monitoring Service, Version 3, 2021) and "terra" package (Hijmans et al., 2022). TRI measures the terrain heterogeneity by calculating the sum change in elevation between a grid cell and its eight neighbor grid cells (Riley et al., 1999). TWI indicates areas with accumulating water flow, and it is an important tool for showing the geomorphic complexity of a landslide terrain, also including the pattern of topographic highs and lows for indicating the dry and wet areas, respectively (Beven & Kirkby, 1979; Różycka et al., 2017). We then mapped three habitat types in the study area: grasslands, forests, and rocks. We used high-resolution satellite imagery (Copernicus Open Access Hub, Sentinel 2, 2022) and classified the habitats into the three types by training the algorithm of the classification tool in the Geographic Information System (GIS) with 50 polygons per habitat type. We finally calculated three distance metrics, measuring the closest distances of chamois observations from (a) escape terrain, (b) roads (paved and unpaved), and (c) hiking trails. We defined as escape terrain the polygons satisfying a steep slope above 45^0 and an area above four grids (>2,500 m^2). We considered the road network in the study area (138 km of roads) (data from Biodiversity Conservation Lab used to define the national roadless map (Kati et al., 2023b) and the network of hiking trails (305 km of trails) (Hellaspath, 2022). We used the "distanceto" package (Miller et al., 2019) in R for all distance calculations.

Data analysis

Calculations of data treatment and analysis were performed using Arc GIS Pro (version 3.2, 2023) and R program (version 4.3.0) (R Core Team, 2023).

Seasonal and annual range

For the seasonal and annual ranges of the population, we performed Kernel Density Estimates (KDE) to map the utilization distribution of the species using the "adehabitatHR" package (Calenge, 2006). We determined chamois seasonal and annual ranges using the 95% Fixed Kernel density estimation, which implies a probability of species occurrence in its range greater than 95% (Worton, 1989). We also used a precise ecological model of spatial utilization to objectively delineate core areas, namely areas of intense use within which an animal spends a maximum amount of time (Vander Wal & Rodgers, 2012).

Population density and demography

To estimate the chamois population density on Mt. Olympus, we divided the number of individuals by the annual range of the species. We also estimated the ratio of males/females (sex ratio) and the ratio of kids/females (fecundity rate).

Seasonal habitat selection

We used the Ecological-Niche Factor Analysis (ENFA) (Hirzel et al., 2002), to explore the seasonal habitat preferences of the species versus available habitat (nine environmental variables). The ecological niche of the species consists of two components within the ecological space: marginality and specialization. The marginality measures the differentiation of the average conditions in the habitat used compared to available conditions in the study area. The specialization measures the niche breadth of the habitat used and reflects the species' tolerance for changes in environmental conditions. We included all variables in the model (Spearman's $|r| \leq 0.75$), and we used all direct and indirect observations per season as presence points (utilized habitats) and a set of 1,182 random points across the study area (available habitat). We finally identified the degree to which every variable contributed to the marginality and specialization in terms of their respective contribution score to the corresponding axes. Statistical significances were tested with the Monte-Carlo randomization procedure (1,000 iterations). For the analysis, we used the "adehabitatHS" package (Calenge, 2011b).

Results

Our chamois dataset included 1,182 observations collected during the seasonal chamois surveys (48% direct observations of animals and 52% of tracks and pellets) (Appendices, **Table 2A.1**).

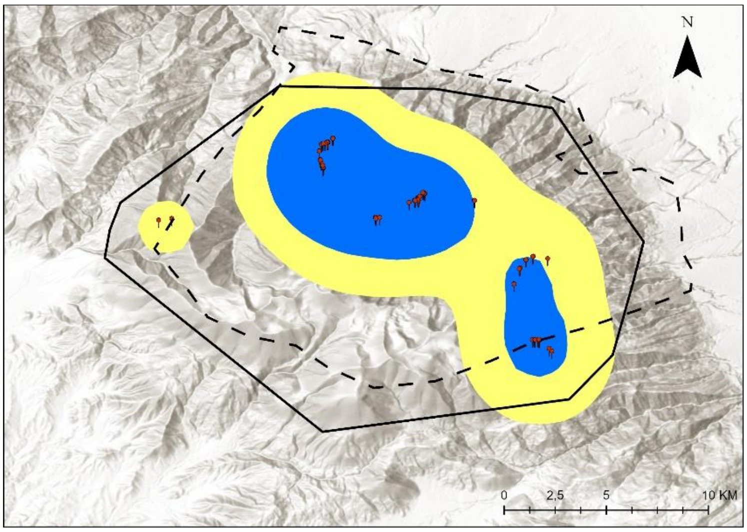
Seasonal and annual range

The annual range of the Balkan chamois on Mt. Olympus covered an area of 103 km^2, accounting for 42% of the study area, and the merged area of all seasonal ranges was 242 km^2 extending over the study area (**Table 2.1**, **Fig. 2.2**). The annual core area was 33 km^2 (13% of the study area). Chamois presented the smallest seasonal range in autumn, followed by summer and then spring, and the largest seasonal range in winter-the same pattern applied to the respective core areas (**Table 2.1**, **Fig. 2.2**).

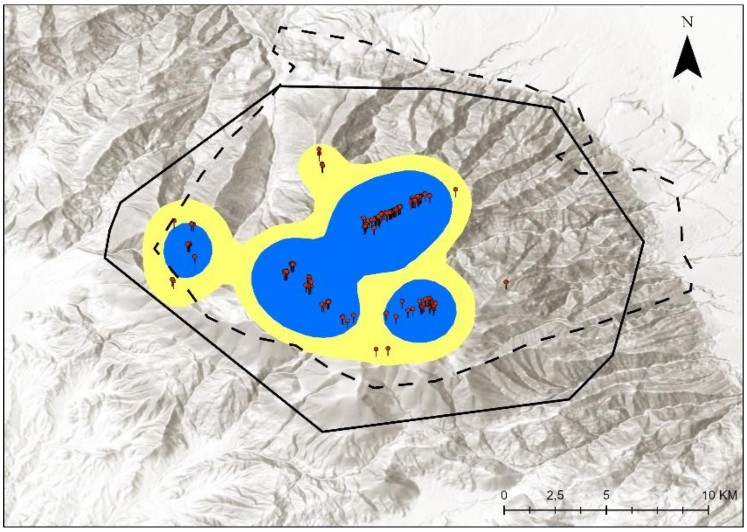
Table 2.1 Seasonal and core area ranges and seasonal habitat description in terms of average values of environmental variables and frequency (%) of observations per season, of the Balkan chamois on Mt. Olympus. The range of values is also provided for the study area

Variable	Spring	Summer	Autumn	Winter	Annual	Study area
Seasonal ranges (km^2)	140.3	86.2	43.2	201.2	103	-
Core area ranges (km^2)	51.4	43.5	35.6	51.8	33.4	-
Elevation (m)	2,050	2,448	2,459	1,823	2,141	297-2,918
Forest (%)	38.4	2.4	0.1	51.5	25.8	55
Grassland (%)	36	78.4	78.1	25.1	51.6	27
Rocks (%)	25.6	19.2	21.7	23.4	22.475	10
Terrain Ruggedness Index	8.06	7.48	6.45	10.31	8.38	0-695
Topographic Wetness Index	44.4	56.49	61.25	42.81	52.03	0-255
Distance from road (m)	1,879	1,830	2,560	1,228	1,894	-
Distance from trail (m)	31	174	134	81	107.5	-
Distance from escape terrain (m)	256	400	495	314	404.5	-

a) Spring range: 140.3 km^2



b) Summer range: 86.2 km^2



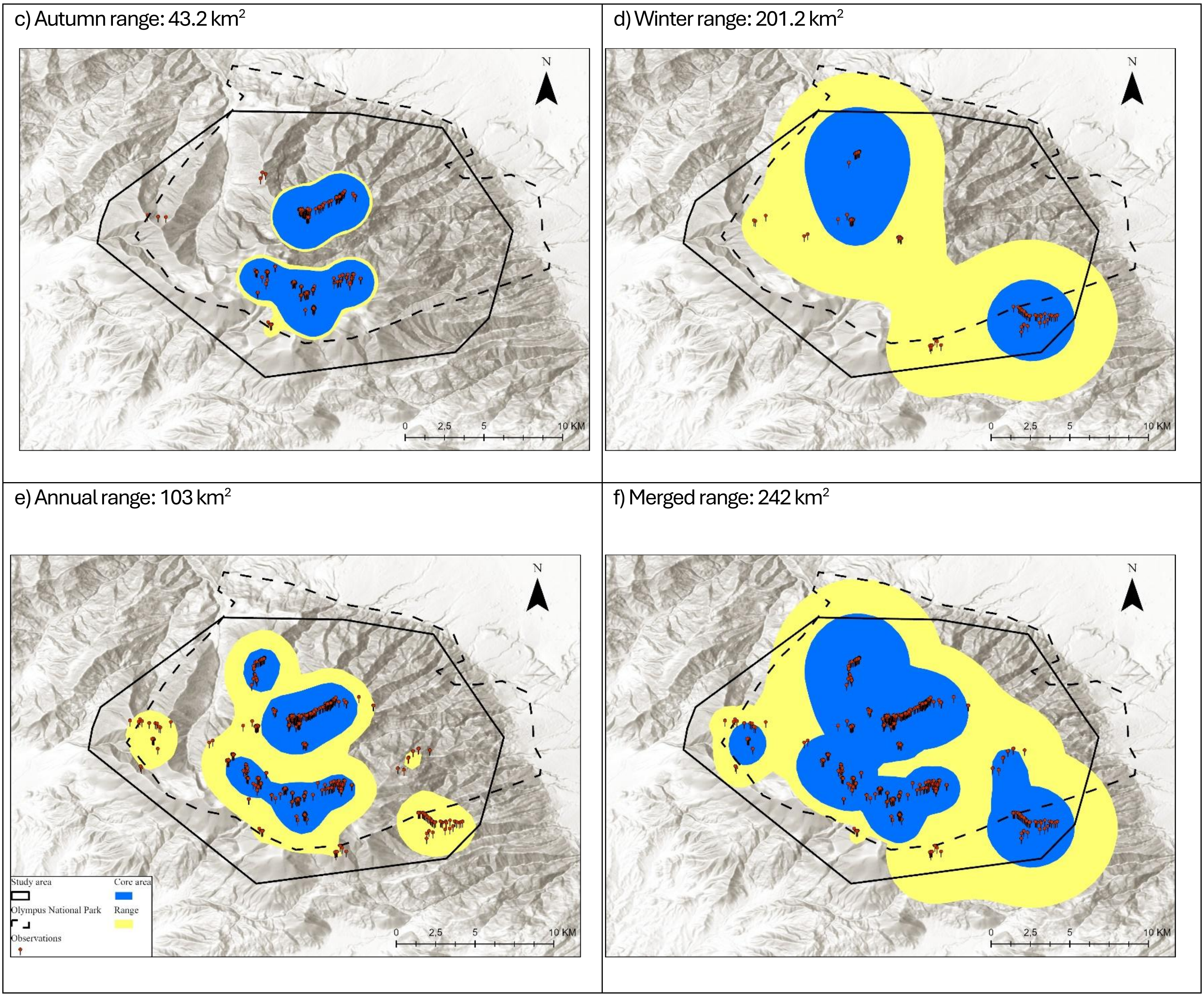


Fig. 2.2 Seasonal ranges and core areas: Seasonal ranges (yellow) and the respective core areas (blue) based on chamois observations in 2022–2023 on Mt. Olympus, concluding with the annual range (and the merged seasonal range)

Population size and demography

We counted 430 individuals during the autumn survey (2022). The population density was 4.2 individuals/km^2. The greatest proportion of the population was adults (71%), followed by yearlings (16%) and kids (13%). The ratio of males/females was 0.35, and the fecundity rate was 0.16.

Seasonal habitat selection

The Balkan chamois used habitats ranging from 1,300 m to 2,722 m in the study area (**Table 2.1**). The results of the ENFA analysis revealed that Balkan chamois exhibited distinct seasonal preferences in response to the available habitat on Mount Olympus ($p < 0.001$) (**Table 2.2**). It showed a clear preference for higher elevations across seasons, preferring higher altitudes in summer and autumn (marginality values > 0.47) and did not tolerate changes in this pattern (specialization values >0.51) (**Table 2.1**, **Table 2.2**, **Fig. 2A.2**). The species also consistently preferred to be near hiking trails, mainly in winter and spring. On the other hand, it constantly avoided roads, but less so in winter. The Balkan chamois preferred grassland areas and avoided forested areas during summer and autumn, and areas with rocky terrain in proximity to escape terrain during spring and winter. The escape terrain extended over an area of 9.3 km^2 in the study area (4%) (**Fig. 2A.3**). At fine scale (30 m grid), the Balkan chamois showed a slight preference for localities with milder topography (TRI marginality values), not tolerating changes to this pattern (specialization values >0.51). The wetness of the terrain (TWI) had a limited role in the habitat selection pattern of the chamois (**Table 2.2**).

Table 2.2 Habitat selection of the Balkan chamois on Mt. Olympus, according to Ecological Niche Factor Analysis

		Spring		Summer		Autumn		Winter	
Code	**Variable**	**M**	**S**	**M**	**S**	**M**	**S**	**M**	**S**
E	Elevation	0,36	0,25	0,51	0,50	0,47	-0,63	0,25	0,41
F	Forest	-0,15	0,36	-0,52	0,40	-0,48	-0,48	0,10	0,30
G	Grassland	0,22	0,06	0,47	-0,12	0,40	-0,09	0,02	0,11
R	Rocks	0,35	0,12	0,22	-0,01	0,19	-0,01	0,46	0,17
TRI	Terrain Ruggedness Index	-0,19	0,51	-0,16	0,75	-0,19	-0,61	-0,14	0,78
TWI	Topographic Wetness index	-0,13	0,11	0,09	-0,09	0,14	-0,07	-0,24	0,10
Dr	Distance from road	0,49	0,21	0,30	-0,05	0,47	0,00	0,14	-0,21
Dt	Distance from trail	-0,56	0,65	-0,26	-0,02	-0,29	0,01	-0,71	-0,03
De	Distance from escape terrain	-0,28	0,22	-0,10	-0,03	-0,01	-0,04	-0,33	0,22

M: marginality, S: specialization.

Discussion

Methodological insights and limitations

In our study, we used high-resolution imagery and trained an algorithm to map three main habitat types on Mt. Olympus reliably, with the help of GIS. We suggest using this approach to map habitats locally in the case that other cartographic backgrounds, such as the maps of land uses of Corine Land Cover (European Environment Agency, 2023) or NATURA 2000 habitat maps (EIONET, 2019), are unreliable or too coarse for fine-scale habitat selection studies. The habitats identified during fieldwork aligned with the habitats mapped by the algorithm. We also introduced a new concept for escape terrain definition, adding the parameter of the extent of the terrains of steep slopes to the single parameter of slope steepness used so far (Bhattacharya et al., 2022; Khan et al., 2016; Sarmento & Berger, 2020). We suggest considering a threshold of minimum area of cliffs and steep terrains (>45°) of at least 2,500 m^2 to define and map the escape terrains in chamois habitats, securing adequate protection for the species. In absence of telemetry equipment, we used the number of observations to delineate the seasonal ranges and respective core areas of intense use at the population level. However, chamois movement ecology should be explored at the individual level (GPS-tagged animals), allowing the delineation of individual home ranges and a more accurate delineation of the areas of intense use at both individual and population levels.

Annual range

We found that the annual range of the Balkan chamois on Mt. Olympus was extended (103 km^2) as compared to other Greek mountains (65 km^2 on Mt. Timfi (Kati et al., 2020) and 55 km^2 on Mt. Giona (Papaioannou et al., 2015)), indicating a large extent of suitable habitats for the chamois in combination with the low disturbance on the species.

Mediterranean seasonal range pattern and global warming

Our analysis showed that the smallest seasonal range was observed in autumn. This was expected, as autumn is the rutting season and the chamois presents an aggregative pattern for reproduction (Corlatti et al., 2022b). However, we found that summer was the second season with the smallest range and core area and not winter as is widely evinced for European populations (Crampe et al., 2007; García-González et al., 1992; Nesti et al., 2010), including one in Greece (Kati et al., 2020). The typical "Continental" seasonal distribution pattern known so far for European chamois populations implies that the species searches for microhabitats of milder climatic conditions and greater food availability to cope with the harsh winter conditions, explaining the restricted seasonal range of the species during this period. Winter is considered the stress period for the species, characterized by low forage quality of food resources (Corlatti et al., 2023) and increased kid mortality (Gonzalez & Crampe, 2001). On the other hand, the inverse "Mediterranean" seasonal pattern implies that summer is the stress period; animals retreat to cooler microhabitats at higher altitudes, near ice remnants or northern-facing slopes, searching for fresh, palatable grass resources of higher forage quality and hence presenting a restricted summer range. This pattern has been reported for the first time for the southernmost Greek chamois population on Mt. Giona (Papaioannou et al., 2015), and Mt. Olympus illustrates the second case. Drought substantially affects Mt. Olympus: it has no lakes and streams above 1,000 m and presents low annual precipitation (841 mm) due to the rain shadow phenomenon, as compared to other mountains in the west (Mt. Timfi: 1,191 mm) or the south (Mt. Giona: 1,560 mm).

We believe other chamois populations might change their seasonal range pattern from Continental to Mediterranean, with the populations in the Mediterranean being most likely to follow it due to global warming. The Mediterranean basin experiences already increased drought (Toreti et al., 2024), and summer warming is expected to exceed the global mean by 40%, associated with high temperatures and heat waves, while a reduction of summer precipitation by 10-15% is predicted for an atmospheric temperature increase of 2°C (Cramer et al., 2018). Drought is known to reduce forage nutritional value in terms of higher plant C:N ratios and lower fiber digestibility (Arroyo et al., 2024), increasing the stress metabolites of chamois during summer (Corlatti et al., 2023). To survive the new conditions, chamois in warmer climates might adopt a strategy of shifting their summer range to higher altitudes, as is the case with the Southern Chamois (*Rupicapra pyrenaica ornata*) (Lovari et al., 2020) and restricting it to cooler microhabitats with higher forage quality according to the Mediterranean pattern. Other Northern chamois populations might also shift their range to higher altitudes and lose a substantial part of their suitable habitat by the end of the 21st century (Hoste et al., 2024). A second strategy might be to remain in the forested zone or select microhabitats with denser tree cover and northern-facing slopes during summer for better thermoregulation (Anderwald et al., 2024). In Greece, chamois have been observed during summer to drink water from the rivers at the bottom of forested river gorges (Aoos and Aracthos gorges), indicating that some animals prefer to remain in forested zones with water availability and avoid the usual annual altitudinal migration (Kati et al., 2020). Another strategy could be to adopt a more nocturnal behavior to avoid extreme temperatures, shifting their activity peak earlier in the morning and increasing their activity at night (Thel et al., 2024). In any case, the responses of animals to global warming are unknown and might be adapted to the different conditions across the European mountains, depending on the trade-offs between thermoregulation, foraging, water availability, interspecific interactions, and human disturbance (Anderwald et al., 2024; Anderwald et al., 2021b; Mason et al., 2014b; Thel et al., 2024).

Population size and demography

According to our findings, Mt. Olympus continues to host the second-largest population of Greece (c. 430 individuals) after the population of Mt. Timfi (c. 469 individuals) (Kati et al., 2020; Papaioannou, 2015). The population might be slightly larger, when considering potentially missing males staying in the lowland forests during the rutting season (Nesti et al., 2010). It accounted for about 30% of the national population size, which reaches 1,548 individuals (range 1,330 -1,765 ind.) (Papaioannou, 2021). The population density on Mt. Olympus (4.2 individuals/km^2) lay between the population densities on Mt. Giona (2 individuals/km^2) (Papaioannou et al., 2015), and Mt. Timfi (7.2 individuals/km^2) (Kati et al., 2020). It is lower than other Balkan chamois populations (Croatia: 17-21 individuals/km^2) (Kavčić et al., 2021a) or other alpine chamois and isard populations reported from European mountain chains (12 to 31 individuals/ km^2) (Allainé et al., 1991; Boschi & Nievergelt, 2003; Corlatti et al., 2013) underlying the perspectives for local population growth. On the other hand, our findings showed a doubling of the species' population size compared to the year 2015, confirming the constant increasing population trend over the last 25 years (Adamakopoulos et al., 1997; Papaioannou, 2021).

Our results showed that the sex ratio of Balkan chamois population on Mt. Olympus was notably skewed in favor of females (0.35), as compared to the population on Mt. Timfi (0.63-0.80) or to Mt. Giona, where the sex ratio was balanced (1.05) (Kati et al., 2020; Papaioannou et al., 2015), in line with other chamois populations in Europe (Bocci et al., 2010; Herrero et al., 2002). This could be explained by the fact that some males may remain in the lower forested habitats during the rutting season, making them less detectable during autumn surveys (Nesti et al., 2010). Another plausible explanation could be that poachers avoid killing females and rather select males, to avoid the population crash.

The ratio of kids/ females was notably low on Mt. Olympus (0.16), being lower than on other Greek mountains and lying outside the typical range for the species (0.55 to 0.85) (Allaine et al., 1990; García-González, 1989; Salzmann, 1977). It is unknown whether the low ratio was incidental for 2022 or indicates a forthcoming trend of deceleration of the population increase. It could be the outcome of low mating success, or it could reflect a high rate of kid mortality due to higher predation or summer aridity stress. Drought led to high kid mortality in mouflon (Garel et al., 2005) and high spring-summer temperatures can reduce chamois yearling body size, likely due to decreased forage quality and availability (Rughetti & Festa-Bianchet, 2012). Preliminary results on the demographic parameters of the species on Mt. Olympus confirm the low ratio of kids/females (0.16) in 2022 and report 15% of summer kid mortality (Papaioannou et al., 2022).Further research is recommended on the mating behavior and kid mortality drivers of the species on Mt. Olympus as well as a systematic monitoring of its population trend.

Seasonal habitat selection vs environmental factors

We found that the animals selected higher elevations on Mt. Olympus throughout all seasons (**Table 2.2**). They followed the typical seasonal migration pattern: moving to higher altitudes in spring in search of better quality grass, occupying gradually the highest available habitats during summer and autumn, and moving again to the lower altitudes in forested zones in winter (Ballo, 2010; Pepin et al., 1992; Trepet & Eskina, 2013).

We also showed that they tended to use rocky areas and areas close to escape terrain during spring and winter (**Table 2.2**), given that rocky areas are usually related to escape terrains. The latter remains an important factor for the habitat selection of chamois, offering the possibility of escape from predators (Elsner-Schack, 1985). Foraging in areas near escape terrain during spring is a common strategy for female ungulates because of the vulnerable offspring (Aycrigg et al., 2021; Bon et al., 1995; Hamel & Côté, 2007). The proximity to escape terrain during winter could be attributed to the greater expected poaching activity this season due to the easier accessibility in the lower forested zone and the reduced number of hikers. On the other hand, the proximity to escape terrain was less pronounced during summer and autumn (400-500 m distance) (Table 1) due to the habituation with hikers.

Furthermore, we found that chamois preferred grassland areas above the tree line during the summer and autumn seasons and preferred the forested zone in winter, consistent with the species' ecology (Corlatti et al., 2022b). However, the preference for forests during winter was less pronounced than in other parts of Europe, where forests function as refuges from extreme weather conditions (Anderwald et al., 2024; De Frenne et al., 2019), which might not be that important in the mild winters of the Mediterranean mountains. The species seems to start the upward movement above the tree line early, as soon as the snow melts, explaining the slight preference for grasslands over forest in springtime.

Finally, we found that the Topographic Wetness index had higher values during summer and autumn in the localities used by chamois (**Table 2.1**), although it was not an influential factor in the habitat selection model. In the case of Mt. Olympus, the index does not reflect water availability in the form of permanent water points due to the limestone bedrock of the mountain, but it might reflect more humid microhabitats. Chamois may favor more humid localities in the search for fresh grass, as animals rely heavily on dew-covered grass in the mornings and residual snow formations to meet their water requirements. Further research is recommended on the impact of forage quality and its water content on the distribution pattern of the species.

Seasonal habitat selection vs anthropogenic disturbance

Habituation with hikers

Our model clearly showed that chamois preferred areas near hiking trails throughout the year. There is no bias from data collection along hiking trails because we conducted a great part of the transects away from hiking trails, and the air distance of chamois observations across transects ranged between 10 m and 3,000 m. The same results for hiking trail preference were obtained when running the ENFA by excluding indirect observations collected only across hiking trails. Notably, this is the first time that such a strong preference is recorded for chamois, as hiking usually has adverse effects on wildlife (Peters et al., 2023). Several herbivore species change their space use (Lesmerises et al., 2017; Thiel et al., 2008) or shift their daily activities (Marchand et al., 2014; Pęksa & Ciach, 2018) to avoid hiking and skiing. Recreational activities can negatively affect animal behavior (Rösner et al., 2014), as observed for mountain goats in ski areas (Richard & Côté, 2016). However, in some cases, chamois are reported to increase their tolerance to human activities by decreasing their vigilance behavior in areas with high levels of nature-based tourism (Schuttler et al., 2017), but the persistence of this behavior can also be fatal during the hunting period (Blumstein, 2016; Courbin et al., 2022) or against predators (Geffroy et al., 2015). In the case of Mt. Olympus, hunting is prohibited, but chamois poaching incidences have been recorded. We attribute this preference for proximity to hiking trails to the discouraging role of hikers' presence in poaching activity. Hiking trails seem to indirectly offer protection from poaching to the species, which is considered the top threat (Papaioannou, 2021), while they could also offer lower mobility costs to the species in terrains of harsh topography. We could also hypothesize that hiking trails offer protection against other predators, such as the grey wolf on Mt. Olympus, but this does not seem to be the case. Wolves show a preference for forest roads and gentler slopes in Greece, like those of hiking trails and they avoid humans not spatially, but by adopting a nocturnal behavior in areas of high human disturbance (Petridou et al., 2023).

Road avoidance pattern

We found that the chamois consistently avoided roads on Mt. Olympus, apart from wintertime (**Table 2.1**, **Table 2.2**). This pattern was reported for Mt. Timfi, where the species concentrated in the most remote parts of the mountain, away from roads and villages, to avoid poaching and human disturbance (Kati et al., 2020). The species did not need to avoid roads during wintertime on Mt. Olympus, as most upland forest roads are inaccessible due to snow cover. New road construction can diminish habitat area and quality while increasing human disturbance, and ungulates typically tend to avoid road infrastructure across various ecosystems worldwide (Bleich et al., 2009; Lian et al., 2012).

Conservation implications

The primary threats of the Balkan chamois are poaching, competition with livestock, interbreeding with Alpine chamois (*R. r. rupicapra*), habitat loss, and insufficient cross-border coordinated management (Corlatti et al., 2022c). The National Action Plan for the Balkan chamois in Greece (Papaioannou, 2021) is aligned to a great extent with Bulgaria's national action plan (Avramov & Valchev, 2010), and addresses these threats along with additional challenges specific to Greece. It suggests seven main conservation measures, each of which is further divided into various subcategories: population conservation and enhancement, habitat conservation and improvement, conservation and expansion of the distribution range while limiting fragmentation, legislation and policy development, monitoring and research initiatives, public awareness, and international cooperation.

Our work provided further evidence supporting the implementation of the action plan. First, our study corroborated the road avoidance pattern of Balkan chamois in Greece, supporting the three suggested measures of the action plan related to the control of the existing roads that give access to the habitats of the species, the maintenance of roadless areas and the discouragement of land consuming projects in the distribution range of the species. Banning road and artificial land generation in remote mountainous ecosystems has already been implemented in nine mountains of Greece (Kati et al., 2023b; Kati et al., 2022), already benefiting four chamois populations occupying these mountains. Preserving the habitats of the species as roadless areas or as non-go-to areas for development projects is of primary importance, given the recent rapid development of wind-energy investments in protected areas and mountainous ecosystems in the absence of sustainable spatial planning (Kati et al., 2021b), which is expected to lead to rapid land artificialization and habitat loss for montane species (Kati et al., 2023a). We call for prioritizing this measure when implementing the chamois action plan (Papaioannou, 2021), as a flexible, non-expensive, and efficient measure that would greatly favor the species population nationwide.

Second, our findings on the Mediterranean range use pattern linked to the summer aridity stress support the suggested measure of securing water availability to chamois populations through the maintenance of natural sources and water points or the generation of artificial waterholes exclusively for wildlife in arid mountains. Such interventions would reduce the drought stress for the species while likely generating more humid microhabitats of greener vegetation locally. They should be implemented as a priority in the most arid mountains occupied by the species such as Mt. Olympus.

Third, we showed that hiking does not seem to be a problem for the chamois population on Mt. Olympus, discouraging poaching. Nature-based tourism in protected areas, with activities such as hiking and skiing, has greatly increased in recent years (Balmford et al., 2015), but the number of hikers in Mt. Olympus is reported to be very high but never assessed. We underline the value of implementing coordinated actions for managing the recreational activities in the core habitats of the species, as suggested in the action plan. A visitor management plan should be implemented on Mt. Olympus, assessing, monitoring, and controlling the number of hikers, while promoting public awareness of non-disturbance rules for chamois and its habitats.

Fourth, our results showed that Mt. Olympus holds extended adequate habitats for chamois, as the species presents an extended annual range, but its population size is comparatively low. The perspectives for further population growth are positive, but well-coordinated actions are needed, targeting the reduction of poaching and the enlargement of the hunting banning zone to cover the merged seasonal ranges, in line with the suggested measures of the action plan for the preservation of the distribution range of the species (Papaioannou, 2021).

Finally, further research is recommended for the mating behavior and kid mortality drivers of the species on Mt. Olympus to elucidate the low fecundity rate recorded, for the impact of global warming on forage quality and water content of feeding sources of the species, as well as a systematic monitoring of its population trend. The implementation of conservation measures for Mt. Olympus is of primary importance, given the Olympus population is isolated and genetically differentiated, forming one of the six chamois population blocks in the country (Papaioannou et al., 2019).

Conclusions

The current work contributes new ecological and methodological insights for the implementation of the national action plan to improve the conservation status of the Balkan chamois in Greece. We suggest the use of high-resolution imagery and algorithm training for the mapping of chamois habitat types, and the consideration of both slope steepness and extent in the definition and mapping of the escape terrain of the species at a national scale. The Mediterranean range use pattern found on Mt. Olympus implies that the stress period for the Balkan chamois in arid mountains is summer and not winter and we call for further research on the effects of global warming in Mediterranean chamois populations. The strong road avoidance pattern and the preference for proximity to hiking trails are both considered tactics of the species for poaching risk minimization. The habitat selection results were in line with the species ecology, following the typical seasonal migration pattern, and favoring proximity to escape terrain, though its dependence on forests seems to be less pronounced during the cold season. This piece of work fully supports the conservation measures suggested by the national action plan.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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CRediT authorship contribution statement

Konstantinos Papakostas: data curation, formal analysis, funding acquisition, investigation, methodology, software, visualization, writing-original draft, writing-review and editing.

Haritakis Papaioannou: investigation, data curation, validation, writing-review and editing.

Marco Apollonio: methodology, writing review and editing.

Vassiliki Kati: conceptualization, methodology, project administration, resources, funding acquisition, supervision, writing-original draft, writing-review and editing.

Ethics statement

Fieldwork was conducted under the permit of the Ministry of the Environment and Energy (ΥΠΕΝ/ΔΔΔ/20036/756, date: 28/03/2022).

Data availability

Due to the protected status of the species, georeferenced data of chamois are sensitive and not publicly available.

Appendices 2

Table 2A.1 Dataset of Balkan chamois' observations on Mt. Olympus during the fieldwork

Season	Animals	Pellets	Tracks	Total
Spring	9	78	7	94
Summer	124	115	11	250
Autumn	401	252	14	667
Winter	35	110	26	171
Total	569	555	58	1,182

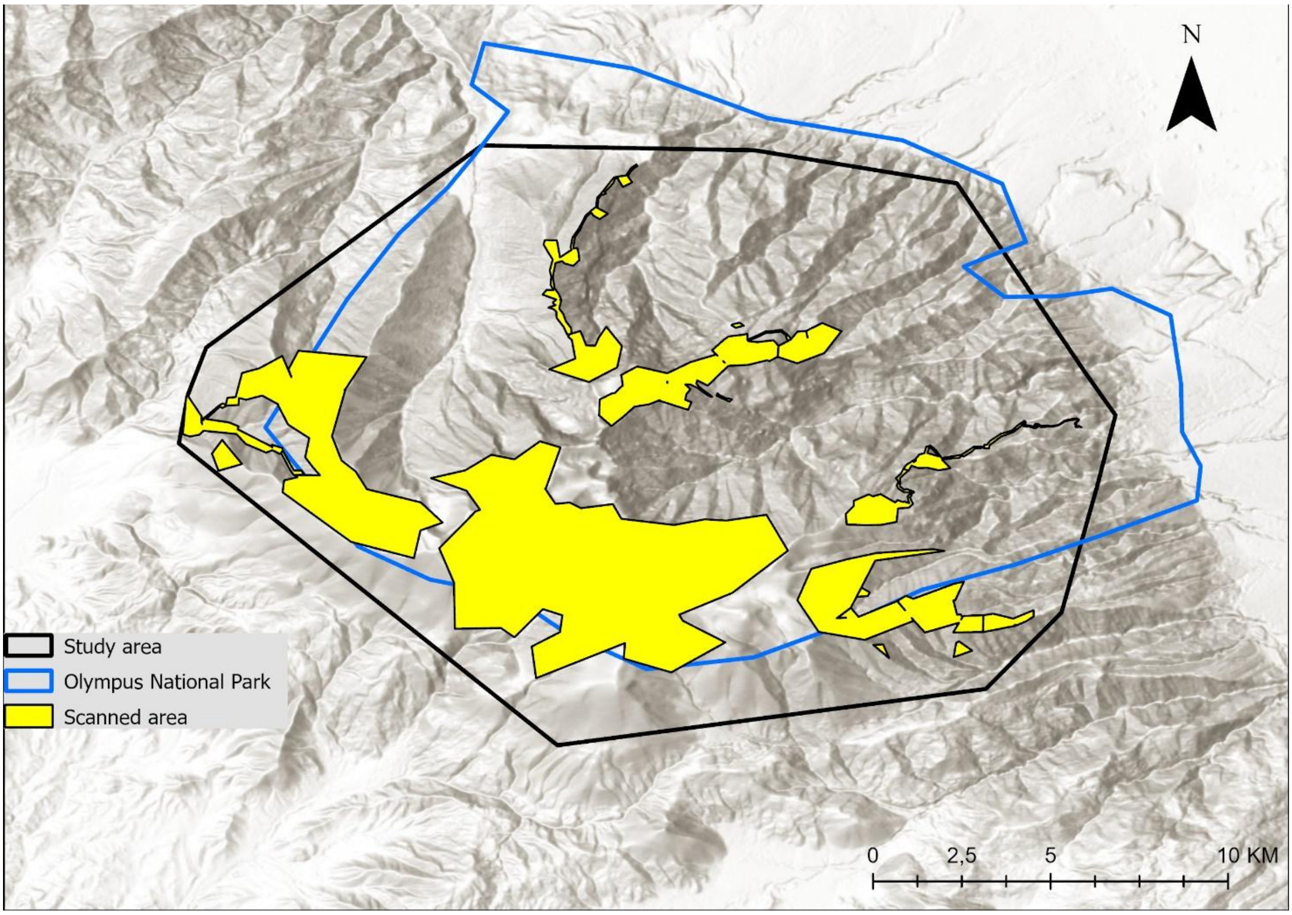

Fig. 2A.1 Area scanned across transect surveys of 2022-2023 on Mt. Olympus

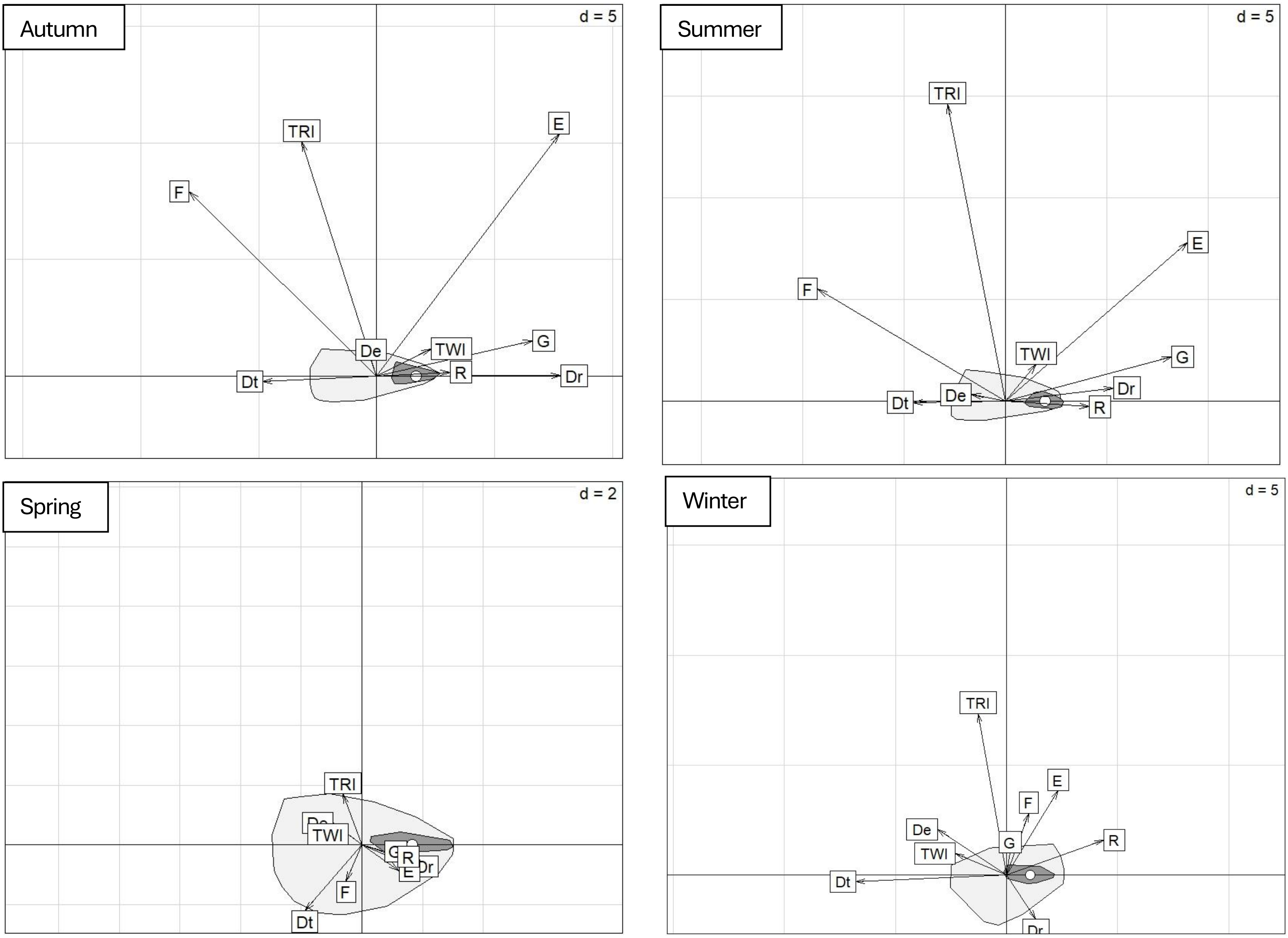

Fig. 2A.2 Ecological Niche Factor Analysis (ENFA) biplots for the seasonal habitat selection of the Balkan chamois on Mt. Olympus. Light gray: available habitat. Dark gray: used habitat. White dot: centroid of the used habitat. E: Elevation, F: Forest, G: Grassland, R: Rocks, TRI: Terrain Ruggedness Index, TWI: Topographic Wetness Index, Dr: Distance from road, Dt: Distance from trail, De: Distance from escape terrain

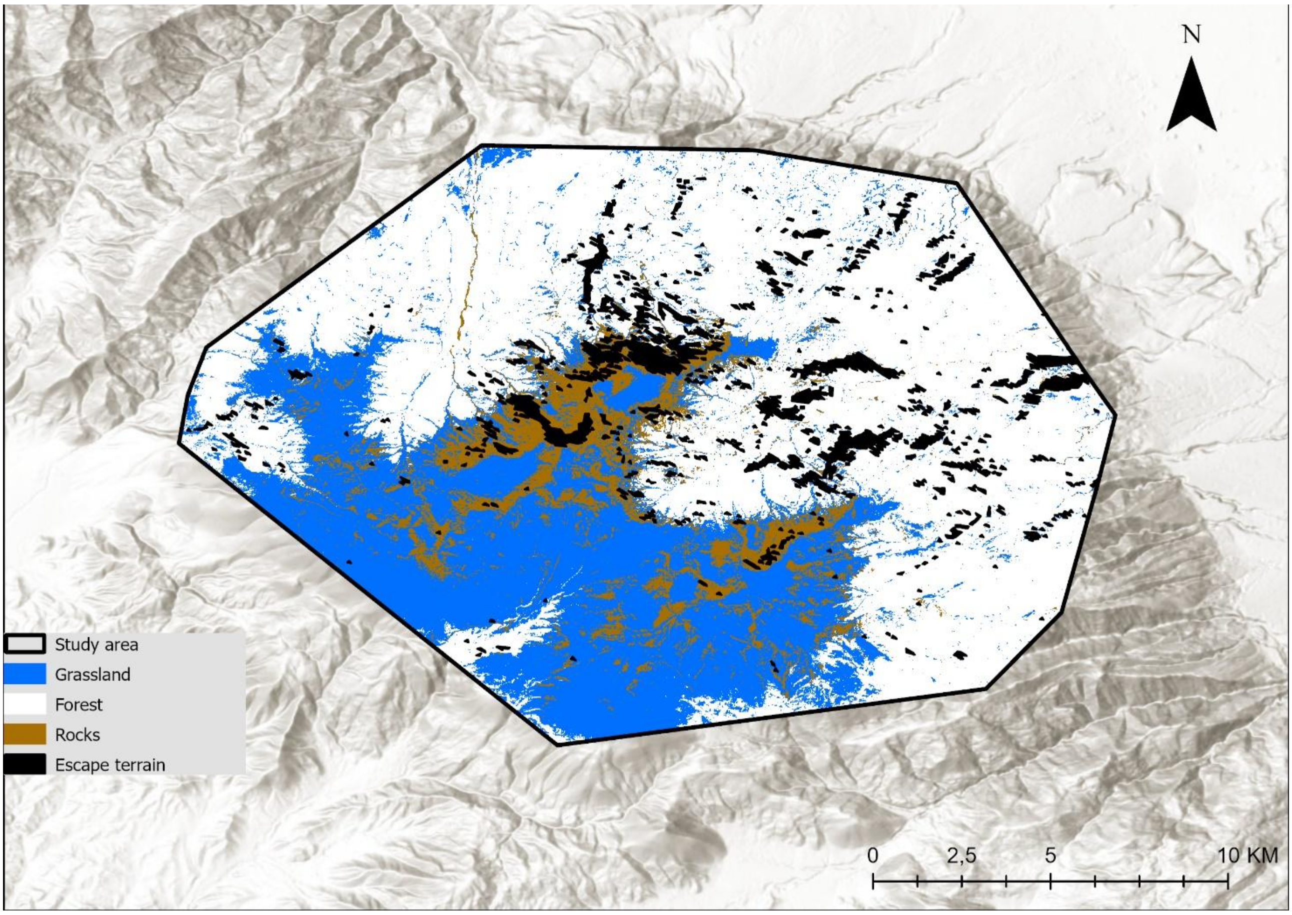

Fig. 2A.3 Escape terrain of the Balkan chamois in Mt. Olympus defined as polygons with a steep slope above 45^0 and an area above 2,500 m^2

Chapter 3. Mapping Balkan chamois habitat use and assessing human disturbance and renewable energy impacts on Mount Oiti, Greece

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Abstract

The Balkan chamois (*Rupicapra rupicapra balcanica*) is a protected ungulate with poor conservation status in Greece. We conducted seasonal surveys (2023) to collect 652 species' occurrences on Mt. Oiti (study area: 156 km^2). The seasonal ranges and the respective core areas (Kernel Density Estimates) showed limited size variation and a great spatial overlap, indicating limited seasonal movements. The suitable habitat (suitability values ≥0.6) as defined by Species Distribution Models (SDMs) covered 12.2 km^2, with 28% extending beyond the Natura 2000 network of protected areas. The chamois inhabited forests throughout the year, besides grasslands in the summer and autumn. The three variables contributing most to the SDMs were related to human disturbance. The species strongly avoided areas near livestock pens, roads, and hunting grounds. Three wind power stations are planned; if constructed, the species will lose 17% of its suitable habitat and could reduce its range. The impact of nine proposed small hydroelectric stations remains uncertain. These findings emphasize the need to avoid infrastructure and road construction in suitable chamois habitats, expand protected areas and wildlife refuges, and manage livestock activities, supporting the implementation of the national action plan for the species.

Keywords

Rupicapra, Distribution range, Forest, Habitat selection, Habitat suitability, Hunting, Livestock, Wind Power Stations

Introduction

Human disturbance profoundly impacts wildlife through multiple mechanisms, including habitat loss and alteration due to infrastructure development, pollution, and climate change. It also directly reduces population densities through hunting and harvesting, creates anthropogenic landscapes of fear, and reshapes biological communities by introducing predators or pathogens (Gaynor et al., 2024). Ungulate species have developed several human-avoidance strategies, including increased nocturnal activity (Gaynor et al., 2018; Petridou et al., 2023), reduced movement range (Tucker et al., 2018), and modifications in resource use patterns (Ciach & Pęksa, 2019; Gaynor et al., 2024; Richard & Côté, 2016). Furthermore, human-driven global warming is expected to shrink the range of mountain ungulates by pushing them to higher elevations or into forests to escape rising temperatures (Lovari et al., 2020; Reiner et al., 2021).

Gaining a deeper understanding of the ecological requirements of the species vis-à-vis the human-induced pressures is essential for mitigating threats, and habitat suitability models serve as a key tool in this effort. These models analyze the relationship between species occurrences and environmental and human disturbance variables, concluding with mapping the suitable habitat for the species and pinpointing the key factors shaping it (Guisan et al., 2013). Such predictions provide valuable insights for conservation management and planning. For example, they can guide decision-makers to designate protected areas, predict range shifts due to climate change, and accomplish restoration projects (Angelieri et al., 2016; Rondinini et al., 2005; Salas et al., 2018; Villero et al., 2017).

One species of conservation concern that has been nationally prioritized to benefit from such conservation actions is the Balkan chamois (*Rupicapra rupicapra balcanica*). Its global population is less than 10,000 individuals across nine countries, with 1,330–1,765 individuals in Greece across 30 populations, showing an increasing national population trend (Anderwald et al., 2021a). It is protected under European legislation (listed in Annexes II and IV of the Habitats Directive 92/43/EEC), but its conservation status in Greece is poor and classified as Inadequate-Bad (U2) (EIONET, 2019), despite its hunting prohibition for over fifty years. For this reason, a national action plan for population recovery has been compiled and approved for implementation (Papaioannou, 2021). According to the action plan, approximately 7,409 km^2 of Greece (5.6% of the national territory) qualifies as a potential habitat for chamois. Still, chamois currently occupy only about one-quarter of this area (1.5% of Greece), and the quality of these habitats has not yet been evaluated. Synergistic pressures from chamois poaching, new road construction and hunting of other species predominate, while additional pressures include competition with livestock in mountainous pastures, tourism, mining, genetic isolation, and climate change (Papaioannou, 2021).

The current study focuses on the Balkan chamois population on Mt. Oiti, a renowned mountain for its flora diversity and endemism (Karetsos et al., 2018), hosting a rich fauna (Mertzanis et al., 2016) and being protected as a National Park since 1966. The mountain is located near Mt. Giona, both occupying the southern part of the Balkan chamois distribution range. A particular "Mediterranean" seasonal distribution pattern has been reported for Giona, with the population aggregating around the highest available summits during summer, to overcome the aridity stress imposed by the warm summer period (Papaioannou et al., 2015). We explored whether this pattern would also apply to the population of Mt. Oiti, as it is characterized by similar climate conditions of hot and arid summers and mild winters, but on the other hand, it has more extended forests and permanent water availability. The population on Mt. Oiti could follow either the "Mediterranean" pattern (stress period in summer), observed in arid mountains (Mt. Giona and Mt. Olympus) (Papaioannou et al., 2015; Papakostas et al., 2025b), either the typical "Continental" pattern (stress period in winter) observed in cooler and more humid mountains (Mt. Timfi) (Kati et al., 2020), or not to undergo any seasonal stress. We also asked if the population shows forest-dwelling behavior or follows the typical chamois seasonal rotational movement pattern (Corlatti et al., 2022a). This pattern is reported for other populations in Greece: animals inhabit lower forested habitats mainly in wintertime, gradually ascend to open mountainous grasslands above the tree line in summer, and remain there in autumn during the rutting season (Kati et al., 2020; Papaioannou et al., 2015; Papakostas et al., 2025b). We aimed to assess the species' suitable habitat on Mt. Oiti, identify key shaping factors, and pinpoint which anthropogenic pressures outlined in the action plan are present in the area. Furthermore, we discuss the likely impact of planned new renewable energy infrastructures (RAE, 2024) and their potential impact on chamois habitats. There is growing evidence of the cumulative negative impacts of renewable energy infrastructures on wildlife and natural ecosystems, including direct species mortality, habitat loss, degradation and fragmentation, deforestation, erosion, noise and light pollution, disruption of hydrological cycles, and carbon stock loss (Bennun et al., 2021; EC, 2020; Gasparatos et al., 2017). However, the impact of such renewable energy projects on chamois populations has not been studied, and our understanding of the impacts on terrestrial mammals in general remains limited (Perrow, 2017). As the wind energy sector develops fast in Greece, with the country being among the top most attractive renewable markets globally (EY, 2023), our study serves as a typical paradigm of conflicting biodiversity vs renewable energy policies that require sustainable spatial planning solutions (Kati et al., 2021a). We set four objectives for the case study of the Balkan chamois population on Mt. Oiti. We aimed to: (a) explore the annual and seasonal ranges, including core areas frequently used by the population (b) pinpoint the key factors shaping suitable habitat and deliver a habitat suitability map, (c) explore the habitat preferences of the species, and (d) assess the impact of planned renewable energy infrastructure on chamois habitat. We finally discuss our findings from a conservation perspective, in the frame of the national action plan suggested actions (Papaioannou, 2021).

Methods

Study Area

The study area is located on Mt. Oiti in southern Greece (38°49'43''N 22°17'19''E). It covers 156 km^2, aligning with the species range on Mt. Oiti according to the IUCN red list of threatened species (Anderwald et al., 2021a) **(Fig. 3.1)**. It is a mountainous area with a mean altitude of 1,361 m, extending from 92 to 2,152 m (Pyrgos peak) with 81% of its extent being above 1,000 m. The geological bedrock consists mainly of limestone (60%) and flysch (32%), and the mountain is characterized by perennial streams and water bodies (**Fig. 3A.1**). The annual precipitation was 854 mm, and the temperature ranged from −16.4 °C (average of minimum values) to 33.7 °C (average of maximum values) (Data from Vrizes Meteorological Station, 1,250 m: 2020–2022). It is a forested area (76% forest cover), dominated by coniferous forest, mainly of Greek fir forests (*Abies cephalonica*), with a small northeastern area featuring black pine (*Pinus nigra*), according to EUNIS typology (Davies et al., 2004). Broadleaved forests comprise mainly deciduous oak forests (*Quercus* spp.). Mixed forests consist mostly of mixed oak and fir stands in the southern and western parts. Mountainous grasslands dominate at higher altitudes (16% cover) combined with rock and scree patches. Scrubs (5% cover) consist of thermophilous evergreen broadleaved species (*Quercus ilex*, *Pistacia lentiscus*, *Arbutus* spp., *Quercus coccifera*).

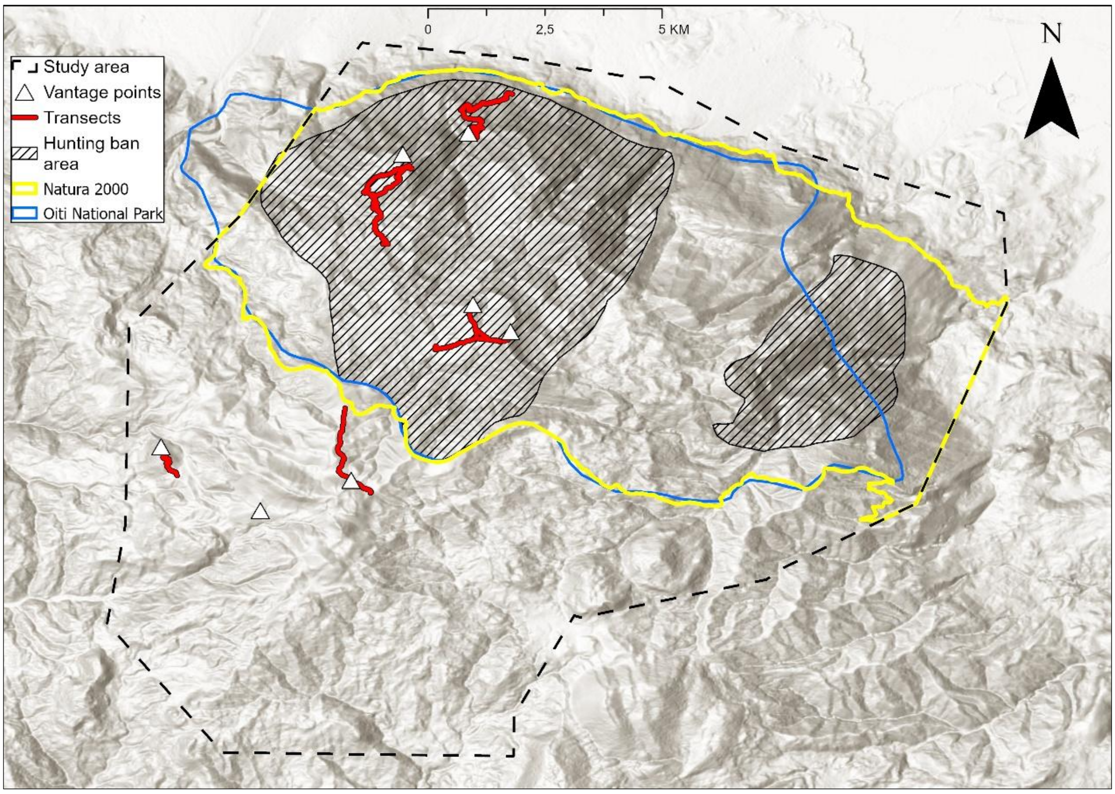

Fig. 3.2 Study area on Mt. Oiti and chamois survey transects and vantage points conducted in 2023. The map shows the borders of Oiti National Park (founded in 1966) and the merged borders of the three Natura 2000 sites within the study area (GR2440003, GR2440004, GR2440007) along with the hunting ban areas (the larger polygon is the core area of Oiti National Park and the smaller the wildlife refuge). Further details in Fig. 3A.3

The Balkan chamois population increased from an estimated 10-30 individuals in the 1980s (Papaioannou & Kati, 2007) to 65-80 individuals in 2016 and shows an increasing trend (Papaioannou, 2021). Other wild ungulate species in the area are the roe deer (*Capreolus capreolus*) and the wild boar (*Sus scrofa*). Chamois predators include the grey wolf (*Canis lupus*) and the golden eagle (*Aquila chrysaetos*). Brown bears (*Ursus arctos*) have also been reported in the area occasionally. Human activities in the study area include mountainous tourism, forestry, and free-ranging cattle and sheep/goat farming that usually takes place from late June to September (9,438 animals accounting for 0.09 Livestock Units per hectare in 2015) (Iliopoulos et al., 2015) **(Table 3A.1)**. Livestock grazing is considered mild in terms of stocking rates, as compared with the national average (Eurostat, 2023).

Over half of the study area (52%) falls within the borders of the Natura 2000 network of protected areas, encompassing three overlapping sites totaling 80.5 km^2 out of the 156 km^2 of the study area **(Fig. 3A.2)** (Protected Planet, 2025). One of these sites (GR2440004) is Oiti National Park, including a strictly protected core area (34.7 km^2) that corresponds to the category II of IUCN (National Park) (Dudley, 2008), where road construction and other developments, hunting, and logging are not allowed. Furthermore, one wildlife refuge (8.5 km^2) overlaps with the three Natura 2000 sites (Protected Planet, 2025), where hunting is prohibited (category IV of IUCN: Habitat/species management area) (Dudley, 2008) The Management Unit of Parnassos and Oiti National Parks and

Protected Areas of Eastern Central Greece of the Natural Environment and Climate Change Agency (NECCA) manages the area. Forest management is undertaken by the Forest Service.

Chamois surveys

We surveyed five transects totaling 24 km in length in conjunction with seven vantage points across all four seasons in 2023, covering all major chamois habitats from 470 m to 2,120 m altitude (**Fig. 3.1**). Each seasonal survey was conducted during seven successive field days (spring: 27/4-3/5; summer: 27/6-3/7; autumn: 22/9-28/9; winter: 7/12-13/12). The four seasons reflected the key phases of the chamois' annual cycle (Pepin et al., 1992): spring (including parturition period, 10/03–09/06), summer (warm period, 10/06–09/09), autumn (10/09–09/12, including the rutting period that starts in November (Corlatti et al., 2022a)), and winter (cold period, 10/12–09/03). Considering the visibility along the transects' line of sight, we effectively surveyed 17% of the study area (26.6 km^2) (**Fig. 3A.3**). With the help of binoculars and a telescope, we collected chamois direct observations (animals) as well as indirect observations (pellets and tracks), and we georeferenced all observations (GPS device). In the case of a group, we recorded each individual separately. Pellets that were not fresh, determined by their color and texture, were attributed to the previous season, and very old pellets were not recorded. Non-filtered occurrence datasets can lead to both geographic and environmental bias, resulting in the over-representation of environmental conditions associated with more heavily sampled areas (Anderson & Gonzalez, 2011). To address this issue, we applied spatial thinning by overlaying a 30 × 30 m grid and retaining only one observation per grid cell, using the "spThin" package in R (Aiello-Lammens et al., 2015). Spatial thinning reduces overfitting and improves model performance by minimizing spatial autocorrelation and sampling bias (Boria et al., 2014).

Data analysis

Environmental variables

We set up an environmental database of ten variables at a 30x30 m scale related to topography, main vegetation types, and human disturbance. We computed three topographic variables (elevation, slope, and terrain roughness) using a Digital Elevation Model (DEM) of 30 m resolution (Copernicus Land Monitoring Service, Version 3, 2021). For slope and roughness calculations, we used the "terrain" function of the package "terra" (Hijmans, 2023) in R. We considered three major vegetation types: forests (G1-G5), grasslands (E1, E2, E4, F2), and scrubs (F5) according to EUNIS typology (Davies et al., 2004) (**Table 3A.2**). We calculated four parameters related to human disturbance. We used the road network (263 km) (OSM, 2025) to generate a GIS layer showing the distance to the nearest road (paved and unpaved) **(Fig. 3A.3).** We also used the available database of livestock pens (50 pens) (Iliopoulos et al., 2015) **(Fig. 3A.3)** provided by the local Management Unit of NECCA and the polygons of the hunting ban areas (data from geodata.gov.gr) **(Fig. 3.1)** to generate two GIS layers of distances to these two features. Furthermore, we mapped the escape terrain as steep ($>45^0$) and extended ($\geq$2,500 m^2) slopes (Papakostas et al., 2025b) and we calculated the distance of the observations from it. We performed the distance calculations in ArcGIS Pro (version 3.1.0) using the "Distance accumulation" tool.

Annual and seasonal ranges

To determine the seasonal and annual ranges of the Balkan chamois on Mt. Oiti, we used the whole dataset of direct and indirect observations for the part of the study area surveyed, and employed Kernel Density Estimates (KDE) and the "adehabitatHR" package (Calenge, 2006) in R, with the 95%

fixed kernel estimation (Worton, 1989). Additionally, we delineated the seasonal and annual core areas, defined as the zones with the highest spatial use intensity (i.e., areas where chamois are likely to spend the most time) (Vander Wal & Rodgers, 2012). We calculated the annual range and core area by merging the four seasonal ranges and core areas, respectively. Calculations of data treatment and analysis were performed using ArcGIS Pro (version 3.1.0) and R program (version 4.3.0) (R Core Team, 2023).

Habitat suitability model

We used the "sdm" package in R (Naimi & Araújo, 2016) to model the species' suitable habitat and deliver the respective habitat suitability map. Initially, we assessed multicollinearity among the variables using the Variance Inflation Factor (VIF) with the "vifstep" function (<3) (Dormann et al., 2013; Zuur et al., 2010). The VIF is based on the square of the multiple correlation coefficient (R^2) resulting from regressing the predictor variable against all other predictor variables and is a more precise method than Pearson correlation (Naimi & Araújo, 2016). Forests, slope, and distance to escape terrain were found to exhibit collinearity with grasslands, roughness, and distance to hunting ban areas, respectively, and were excluded from the analysis.

Since we lacked true absence data, we adapted our presence-only database for use in a presence-pseudoabsence modeling framework by generating pseudoabsence points. To do so, we used the Random Forest (RF) modeling technique and a 1:1 ratio of presence to pseudoabsence points, as recommended for RF models in ecological applications (Barbet-Massin et al., 2012) and allocated 30% of the data as test data for model validation. We used two evaluation metrics to assess model performance: Area Under the Curve (AUC) and True Skill Statistic (TSS). AUC evaluates the ability of the model to distinguish between presence and absence points, with values ranging from 0.5 (random prediction) to 1 (perfect prediction), and is a widely used metric for model evaluation in ecological studies (Fielding & Bell, 1997). TSS accounts for both sensitivity (true positive rate) and specificity (true negative rate), with values ranging from -1 to 1, with 1 indicating perfect agreement and values ≤0 suggesting performance no better than random (Allouche et al., 2006). We then combined the outputs of all RF models to create an ensemble prediction ("ensemble" function) that integrates multiple models, thereby capturing a broader range of projections and generating more reliable habitat suitability forecasts (Araújo & New, 2007). We evaluated the relative importance of the variables included in the model using the Pearson correlation and AUC metrics. Person correlation highlights the direct linear contribution of each variable to the model (Franklin, 2010), and the AUC captures the overall contribution of variables to the model (Lobo et al., 2008), including nonlinear effects and interactions. We adopted this dual approach to ensure a more comprehensive evaluation of predictor importance by integrating complementary aspects of variable effects. Furthermore, we defined suitable areas as those with predicted suitability values greater than the mean suitability across training data (Liu et al., 2013).

Seasonal habitat preferences

We calculated the average value of environmental variables in chamois occurrence points for each season and annually (habitat used). We then produced 652 random points (1:1 ratio of presences vs background points) in ArcGIS Pro and estimated their average values in the study area (available habitat). Using the non-parametric Kruskal- Wallis H-test, we investigated whether environmental variables varied significantly throughout the four seasons. We compared the annual environmental variables between the observed and random datasets (used *vs* available habitat) in terms of the Mann-Whitney U test ($p<0.05$).

Renewable energy plans

We considered the database of the National Regulatory Authority for Energy (RAE) for all renewable energy infrastructure in the study area (RAE, 2024). We then considered the total area of the three wind power station polygons planned in the study area and calculated their per cent overlap with the annual range found, with the species' suitable habitat (suitability values greater than the mean suitability across training data), as well as with protected areas cover.

Results

The dataset included 652 observations of the Balkan chamois on Mt. Oiti, comprising 63 direct observations of animals (9.7%), 541 observations of pellets (83%), and 48 tracks (7.3%) **(Table S3).** After observation thinning 121 chamois occurrences remained and were used for the analysis.

Annual and seasonal ranges

The minimum estimated annual range of the Balkan chamois on Mt. Oiti encompassed an area of 50 km^2 and the annual core area accounted for one-third of it (34.8%). The seasonal ranges and their respective core areas for the part of the mountain surveyed exhibited limited size variation and a great spatial overlap (74-90% and 65-87%, respectively) (**Table 1, Fig. S4**).

Table 1 Annual and seasonal ranges and respective core areas of the Balkan chamois on Mt. Oiti (2023) and their overlap (core areas overlap in parentheses) for the part of the mountain surveyed

Season	Range (km^2)	Core area (km^2)	Core area proportion (%)	Overlap (%) of ranges (core areas)			
				Spring	Summer	Autumn	Winter
Spring	32.9	12.2	37	100	74(75)	74(79)	90(69)
Summer	31.5	11.3	35.9	-	100	85(87)	75(65)
Autumn	36.9	13.6	36.9	-	-	100	77(65)
Winter	36.6	10.7	29.2	-	-	-	100
Annual	50	17.4	34.8	-	-	-	-

Habitat suitability model

The analysis encompassed seven variables. RF models demonstrated high performance, with an AUC value of 0.96 and a TSS value of 0.85. The top three variables contributing most to the model were associated with human disturbance: distance to livestock pens, hunting ban areas, and roads, followed by elevation. The remaining variables, namely terrain roughness, scrubland, and grassland cover, had lower contributions to the predictive habitat suitability model (**Table 3.2**). According to the habitat suitability map (**Fig. 3.2**), suitable habitat areas (values above 0.6 or 60%) covered 12.2 km^2, accounting for 7.8% of the study area (**Fig. 3.3**). A considerable part of the species suitable habitat (27.9%, 3.4 km^2) fell outside the Natura 2000 network.

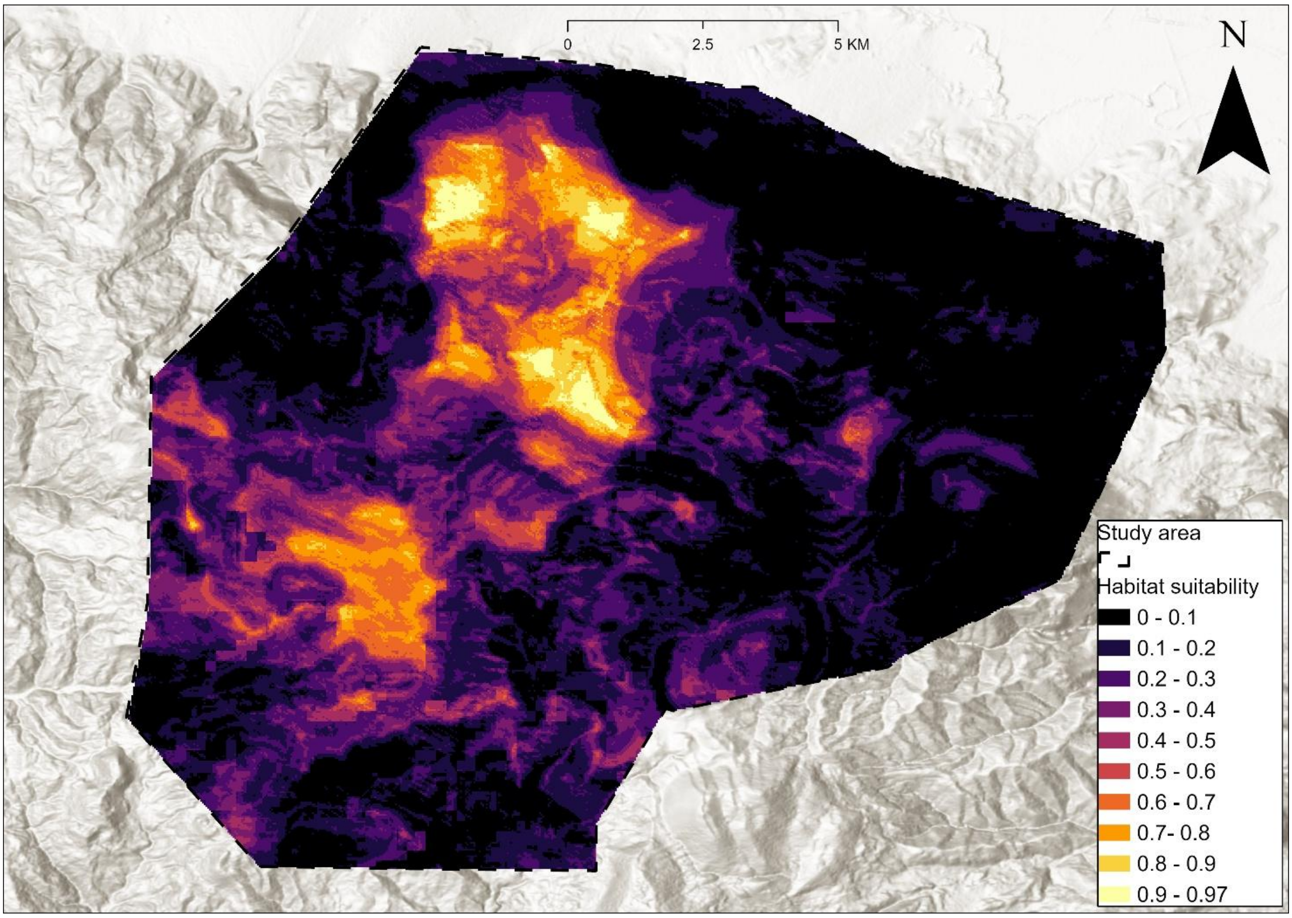

Fig. 3.2 Habitat suitability map of the Balkan chamois on Mt. Oiti, presented in a ten-scale gradient (10% interval)

Seasonal habitat preferences

We found no statistically significant seasonal differences for any environmental variables analyzed (Kruskal-Wallis test, p>0.05). All variables except for three (slope, roughness, and forest cover) significantly differed between observation points and the 1,000 random points in the study area (U tests, p<0.05).

The species preferred higher elevation areas and grasslands and avoided scrublands **(Table 3.2)**. All human-disturbance variables were significantly different in the points of chamois occurrence than random points in the study area. The species preferred areas away from livestock pens, roads, and areas closer to hunting ban areas and escape terrain. However, the latter was only 0.45 km^2, accounting for less than 1% of the study area.

Table 2 Chamois habitat preference: Average values (or frequency percentages) of variables at chamois observation points across seasons and annually compared to 652 random points (R) throughout the study area (Mann-Whitney test, p-values), and variable contribution to the habitat suitability model after Pearson correlation coefficient (P) and Area Under Curve (AUC) criterion

Variable	**Seasons**				**Habitat preference**			**Contribution to the model**	
	Spring	**Summer**	**Autumn**	**Winter**	**Annual**	**R**	**p**	**P**	**AUC**
Elevation	1,568	1,709	1,791	1,780	1,668	1,391	*	14.9	12.8

(m)	(±376)	(±446)	(±315)	(±236)	(±365)	(±487)			
Slope (degrees)	18.2 (±9.7)	14.9 (±6.4)	18.7 (±9)	20.8 (±9.3)	18.4 (±9.3)	17.4 (±8.7)	ns		
Roughness	28.1 (±15.6)	23.2 (±10.9)	28.1 (±14.3)	32.6 (±14.2)	28.5 (±14.8)	26.8 (±15)	ns	2.3	1.7
Forests (%)	92	50	48	83	78	75	ns		
Grasslands (%)	8	50	52	17	22	17	*	1.6	0.8
Scrubs (%)	0	0	0	0	0	4	*	0	0
Distance to roads (m)	548 (±292)	364 (±347)	474 (±422)	618 (±300)	529 (±331)	370 (±330)	*	11.3	7.1
Distance to pens (m)	2,021 (±618)	2,028 (±338)	1,984 (±413)	2,064 (±604)	2,027 (±558)	1,181 (±636)	*	25.4	17.5
Distance to hunting ban areas (m)	353 (±1,031)	71 (±274)	242 (±762)	409 (±1,073)	311 (±942)	1,594 (±1,824)	*	9.8	4.3
Distance to escape terrain (m)	1,973 (±1,948)	1,786 (±1,450)	2,150 (±1,959)	2,568 (±1,898)	2,111 (±1,890)	3,664 (±3,078)	*		

ns: non-significant ($p>0.05$). *: $p<0.05$

Renewable energy plans

The renewable energy plans in the study area include three wind power stations that are currently under a production licensing stage, with a total capacity of 81.6 MW (16 wind turbines of 15.6-34.8 MW each, pylon height of 84-101 m and rotor diameter 131-158 m) and nine small hydroelectric stations (0.48-0.95 MW) totaling 5.6 MW **(Table 3A.4)**. Wind power stations polygons are located outside the borders of Oiti National Park and Natura 2000 network **(Fig. 3.3)**. The area of the wind power stations' polygons covers 6.2 km^2, out of which 61% falls within the annual range of the species found (3.8 km^2) and 33.9% (2.1 km^2) overlaps with chamois suitable (habitat suitability values over 0.6) (**Fig. 3.3**). If they get permission to be constructed, 17.2% (2.1 km^2) of the suitable habitat will be lost on Mt. Oiti. None of the nine hydroelectric stations planned coincide with the current annual range or the suitable habitat of the species. Seven are included in the Natura 2000 network (two of them in Oiti National Park) **(Table 3A.4)**.

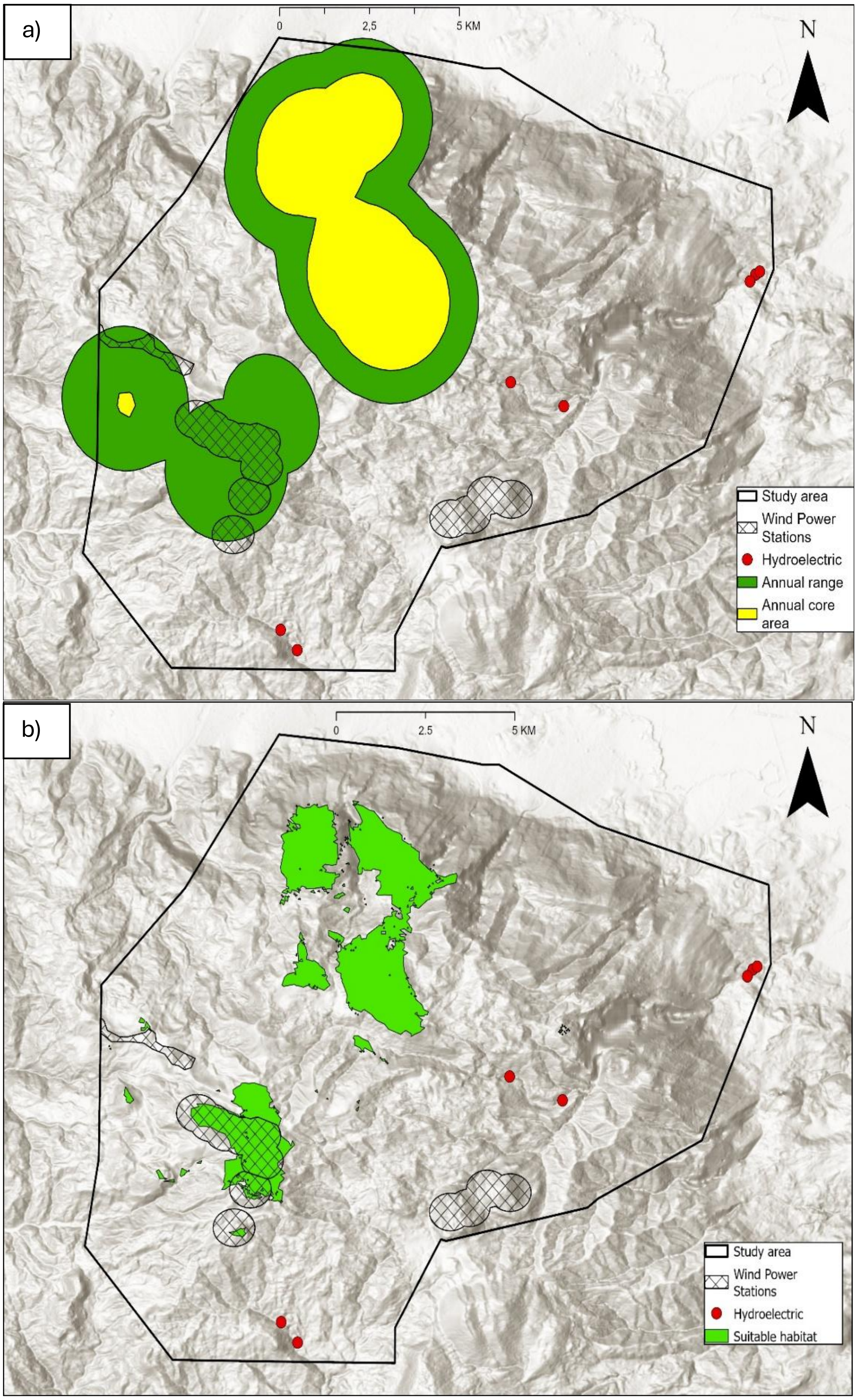

Fig. 3.3 Planned wind power and small hydroelectric stations on Mt. Oiti across (a) the annual range and core area of the species found and (b) suitable chamois habitat (values over 0.6)

Discussion

Methodological insights

Spatial ecology studies employing GPS telemetry data provide highly reliable results for habitat modelling and distribution ranges (Hebblewhite & Haydon, 2010). Without such high-cost equipment, the current research employed field surveys that involved extensive fieldwork. However, two challenges arose: forest cover limited visibility along transects, allowing 17% of the study area to be scanned, and inaccessible terrains due to steep topography, such as areas near the Gorgopotamos Gorge in the eastern part of the mountain, could not be surveyed. Therefore, the annual range is not representative of the whole study area. Our study provided a first insight into seasonal ranges and their core areas of intense use at the population level. Future studies should focus on the movement ecology of chamois at the individual level using GPS-tagged animals to deliver individual home ranges, potentially overcoming the accessibility problem. Such studies could reveal an expanded annual range on Mt. Oiti, as well. The study also delivered a habitat suitability model of adequate performance and allowed us to reliably pinpoint the human factors negatively affecting the chamois habitat use. Other variables, such as solar radiation or exposition were not considered in the modeling process due to scale or data limitation issues, but the latter has been reported not to have a significant effect on habitat use or to be interpreted by other topographic variables, such as the proximity to escape terrain (Kati et al., 2020; Papaioannou et al., 2015). Further research is recommended to delineate the suitable habitat of the Balkan chamois across the Greek mountains and broader spatial scales and pinpoint the common drivers that shape it.

Annual and seasonal ranges

Considering as a study area the species range reported in the IUCN red list of threatened species (Anderwald et al., 2021a), we found that the annual range of the Balkan chamois population on Mt. Oiti covered at least one-third of it **(Fig. 3.2)**. Chamois may also inhabit other parts of the mountains, given fieldwork limitations and the presence of suitable habitats beyond the annual range **(Fig. 3.3)**. In any case, the annual range is dynamic and may shift over time due to changing human disturbance regimes and the species growing population at local and national scales, which gradually results in colonization of new suitable habitats (Papaioannou, 2021).

We found minor range size variation across seasons and a high spatial seasonal range overlap (74-90%) **(Table 3.1)**, implying greater habitat fidelity and limited seasonal movements from lower forested zones in winter to higher altitudes grasslands in summer and autumn **(Table 3.2)**. Likewise, the species on Mt. Oiti does not seem to follow any of the two seasonal distribution patterns reported in Europe or face significant climatic stress. In cooler climates, chamois usually search for adequate microhabitats providing shelter from extreme weather conditions and offering food resources of higher forage quality, resulting in a restricted winter range, according to the "Continental" pattern (Crampe et al., 2007; García-González et al., 1992; Kati et al., 2020; Nesti et al., 2010). In warmer climates, the Balkan chamois seems to retreat to cooler microhabitats that still hold fresh palatable food resources during the arid summer period, justifying the restricted summer range of the "Mediterranean" pattern. This pattern is reported for two populations in Greece, inhabiting the arid mountains of Giona and Olympus (Papaioannou et al., 2015; Papakostas et al., 2025b), but not for the more humid mountain of Timfi in northern Greece, where the species adopts the continental pattern (Kati et al., 2020). Although Mt. Oiti is in the southern part of the species distribution, having similar low precipitation rates to the neighboring mountain of Giona, the population doesn't seem to experience aridity stress. Animals inhabit forested areas throughout the year, benefiting from the extended forests, allowing thermoregulation and providing shelter from extreme temperatures as well as food resources (Anderwald et al., 2024), while also benefiting from the mild winter conditions, and the permanent water availability in streams and water bodies year-round.

Habitat and human disturbance

We found that Mt. Oiti holds extended suitable habitats for the Balkan chamois and that the three top limiting factors shaping the suitable habitats were related to human disturbance. Most reported threats for all chamois species are indeed human-induced, including poaching, overharvesting, habitat loss and degradation, livestock grazing and related disease transmission, and disturbance from human developments, tourism and recreational activities (Corlatti et al., 2022c). According to the national action plan (Papaioannou, 2021), all these threats also apply to the Balkan chamois in Greece, except for overharvesting as chamois hunting is banned, along with specific threats such as road construction, mining, genetic isolation, global warming, and hunting disturbance.

The most influential limiting variable was the distance to the nearest livestock pen; chamois exhibited a significant avoidance pattern away from them. Livestock presence can increase hormonal stress in chamois (Formenti et al., 2018). Livestock avoidance strategy is often a stronger driver than climate change in spatiotemporal behavioral shifts away from suitable habitats and high-quality food resources (Mason et al., 2014b). Besides competition for food resources, livestock presence is associated with disturbance from shepherds' presence and their dogs (Chirichella et al., 2013). Livestock presence occurs seasonally on Mt. Oiti, from late June to September, but coincides with the warm period that chamois occupies high-altitude grasslands. In the absence of livestock activity disturbance and interspecific competition with livestock, it is possible that chamois could use more intensively the mountainous grasslands at higher elevations and present less forest-dependent behavior. Although no infected animals were observed during our surveys, we underline that livestock presence can increase the risks for disease transmission (Fankhauser et al., 2008), which can have substantial impacts on chamois populations (Garrido-Amaro et al., 2023).

We also found a clear preference for chamois to be away from hunting grounds and roads, both related to human disturbance and substantially contributing to the habitat suitability model. Human disturbance does not necessarily relate to human presence *per se*, as the animals on another mountain (Mt. Olympus) do not avoid hikers, but rather prefer to be near hiking trails (Papakostas et al., 2025b). It seems to be more closely linked to the presence of anthropogenic landscapes of fear, generated by legal and illegal hunting activities that involve shotguns use and hunting dogs. For this reason, the species also showed a preference to be near escape terrains, although limited in our study area in extent, to find protection from predators and disturbance (Corlatti et al., 2022b). Therefore, the role of hunting and poaching in the chamois habitat selection process seems to be substantial on Mt. Oiti, as well as other mountains of the country (Kati et al., 2020). Such disturbance is further intensified by forest roads, providing greater public access to chamois habitats, and intensifying hunting and poaching activity. The strong road avoidance pattern of the chamois population on Mt. Oiti appears widespread in Greece and is reported for other populations as well (Kati et al., 2020; Papakostas et al., 2025b).

Three other environmental factors significantly influence chamois habitat suitability. Given the mountainous character of the species (Corlatti et al., 2022b), animals exhibited a preference for higher altitudes, even though their altitudinal range of seasonal migration was limited. Chamois also favored grasslands and avoided scrublands, as also found on Mt. Timfi (Kati et al., 2020). Grasslands offer high forage quality (Gálvez-Cerón et al., 2013) but they are not so extensively used on Mt. Oiti as they could, due to habitat use shifts from livestock presence in the warm period, or the high forage quality inside forests, enhancing the forest-dwelling character of the population.

Renewable energy plans

Our analysis indicated that the proposed wind power station plans overlap substantially with the most suitable chamois habitat on Mt. Oiti. Habitat loss is a major threat to the Balkan chamois throughout its range (Corlatti et al., 2022c). Located at high-altitude grasslands (1,600-2,128 m), the projects are expected to pose significant threats to the local chamois population, primarily through the reduction of grazing grounds, and overall habitat loss and fragmentation. The species might exhibit a range shift away from wind turbines in the study area, probably finding shelter in the most inaccessible forest zones, given its high sensitivity to human disturbance and the adverse wind turbine effects reported for other forest-dwelling ungulates (Schöll & Nopp-Mayr, 2021). While some ungulate studies indicate that wind energy development does not increase mortality risk (Taylor et al., 2016) and does not significantly affect nutrition and home ranges (Walter et al., 2006), other studies document elevated stress near large wind farms (Klich et al., 2020), strong avoidance patterns and changes in the use of movement corridors (Łopucki et al., 2017; Skarin et al., 2015) and even range shifts several kilometers away, outside the visibility zone of wind turbines (Skarin et al., 2018). The adverse effects are associated with both the construction and operation phases of wind turbines (Skarin et al., 2015; Skarin et al., 2018).

The impact of wind energy infrastructure extends beyond habitat loss within the investment polygons (2.1 km^2), where turbines are going to be installed on cement bases. The actual land footprint is larger when accounting for other required infrastructures (transmission lines and electricity pylons, meteorological towers, operation buildings, and new and widened access roads) and the subsequent vegetation clearance required across access roads that would directly impact chamois forest habitats. In Greece, the wind industry causes a 3.5 times higher conversion of natural to artificial land than the global average, due to the tendency to plant wind turbines in remote natural areas with steeper slopes away from existing infrastructures, with access roads being an important land consumer in this process (Kati et al., 2023a). Furthermore, the whole study area exhibits high naturalness and low fragmentation, qualifying it as a wind farm-free zone in a national-scale study for sustainable wind energy planning, excluding such natural areas from wind energy investments without undermining the 2030 national energy goals achievement (Kati et al., 2021a). On the other hand, none of the nine small hydroelectric stations planned fall within chamois suitable habitats. Their impact seems minor but remains uncertain. It is not known whether the stations will affect water availability for wildlife in mountain streams and waterbodies, or the extent of land take expected from road sprawl and infrastructures required.

Conservation implications

Our findings provide strong scientific evidence informing policymaking and conservation actions at local and broad scales as follows: first, we recommend preserving the natural integrity of the study area by preventing land take and habitat fragmentation. This includes discouraging large-scale renewable energy projects, other land-consuming developments, and associated road expansion, given their expected negative impact on the chamois population. These measures are expected to broadly benefit the biodiversity of Mt. Oiti, including endemic and globally threatened insect species that inhabit mountainous grasslands, including the area of planned wind energy investments (Stefanidis et al., 2025). On a broader scale, we advocate for bold policies to protect landscape naturalness and prevent further ecosystem fragmentation from roads and artificial land development. A roadless policy has already been implemented in Greece offering a strict but provisional protection status in nine remote mountains of great naturalness (Kati et al., 2023b; Kati et al., 2022), benefiting four chamois populations there. The government aspires to protect 55 mountains under target 15.4 of the Sustainable Development Goals for mountainous ecosystem maintenance (Hellenic Republic, 2022; UN, 2015). These measures are in line with the national action plan suggesting roadless areas expansion and modification of major construction projects through alternative solutions in the species distribution range (Papaioannou, 2021).

Second, we recommend poaching mitigation measures and the expansion of wildlife refuges to increase the quiet, hunting-free areas that were found to be preferred by chamois. On a broader scale, the national legislation freely allows hunting all over the countryside (with few exceptions), including the protected areas of the Natura 2000 network or private lands when not fenced, as hunting grounds. An accurate national mapping of hunting grounds is missing. Less than 10% of the country is declared a hunting-ban zone for wildlife conservation, covering about 40% of the Balkan chamois' distribution nationwide (Kati et al., 2020), and proving their importance as chamois shelters. Besides hunting-ban areas expansion, we emphasize the need for overall spatial hunting planning, including mapping the hunting grounds, regulating hunting intensity, and implementing government-led monitoring, accounting for chamois and other protected wildlife species needs. This would reduce human-induced "landscapes of fear" and would benefit chamois populations on Mt. Oiti and nationwide.

Third, we suggest drafting and implementing sustainable livestock grazing plans accounting for biodiversity maintenance and chamois needs. Although chamois may benefit from intraspecific competition mitigation, it is still uncertain how the grassland ecosystems and biodiversity will be affected in the long term, since livestock grazing is mild on the mountain and might decrease in the future. Mapping the mountainous pastures of Mt. Oiti, their grazing capacity, livestock stocking density and temporal use, while monitoring the livestock grazing activity on an annual basis is a prerequisite to planning and implementing sustainable grazing schemes favoring both grassland ecosystems, wildlife, and the local economy, in line with the suggestions of the action plan (Papaioannou, 2021).

Data availability

Due to the sensitive nature of the data according to the Greek legislation, and the potential risks associated with disclosing precise locations, the data are not publicly available.

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Declarations

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Conflict of interest The authors declare that they have no conflict of interest.
Ethical approval Fieldwork on Mt. Oiti was conducted under research permission by the Ministry of the Environment and Energy (ΥΠΕΝ/ΔΔΔ/20036/756, date: 28/03/2022).
Consent to participate All authors agreed to participate in this study and all have contributed to its content and current version.

Appendices 3

Table 3A.1 Livestock animals per type on Mt. Oiti based in 2015 (Iliopoulos et al., 2015) and estimation of the Livestock Units per hectare for the study area (15,600 ha). This estimate assumes that all animals graze exclusively within the study area and that no external animals from nearby pens enter the area to graze

Livestock type	Animals	Livestock Unit coefficient	Livestock Units	Livestock Units per ha
Goats	2,375	0.1	237.50	
Sheep	6,449	0.1	644.90	
Cattle	495	1	495.00	
Calf	119	0.4	47.60	
Sum	9,438		1,425.00	0.09

Table 3A.2 Habitat types used in the analysis of habitat suitability for the Balkan chamois on Mt. Oiti, according to EUNIS typology (Davies et al., 2004), their area (km^2) and percent cover (%) of the study area

Habitat	Code	Description	Area (km^2)	Percent cover (%)
Forests	G1	Broadleaved deciduous woodland	13.5	8.6
	G2	Broadleaved evergreen woodland	1.8	1.1
	G3	Coniferous woodland	75.6	48.5
	G4	Mixed deciduous and coniferous woodland	10.2	6.5
	G5	Lines of trees, small anthropogenic woodlands, recently felled woodland, early-stage woodland and coppice	13.9	8.9
Grasslands	E1	Dry grasslands	0.04	0.02
	E2	Mesic grasslands	0.7	0.45
	E4	Alpine and subalpine grasslands	6.1	3.9
Scrubs	F2	Arctic, alpine and subalpine scrub	17.8	11.4
	F5	Maquis, arborescent matorral and thermo-Mediterranean brushes	7.6	4.9

Table S3 Seasonal and total observations of Balkan chamois on Mt. Oiti during 2023 surveys

Season	Animals	Pellets	Tracks	Total
Spring	7	293	18	318
Summer	18	64	11	93
Autumn	28	58	0	86
Winter	10	126	19	155
Total	63	541	48	652

Table S4 Renewable energy infrastructures planned in the study area of Mt Oiti as downloaded from the national database (RAE, 2024), and their technical characteristics, indicating the spatial overlap with the chamois annual range (R), suitable habitat defined by values greater of 60% (H), and the Natura 2000 network of protected areas (N2000)

Renewable energy type	Technical characteristics						Altitude (m)	Spatial overlap (%)		
	Permission stage	Code	Area (km^2)	N	Rotor length (m)	Total capacity (MW)		R	H	N2000
Wind Power Stations	p	36763	3.7	8	131	31.20	2,072	92	57.5	0
	p	36754	2	4	131	15.60	1,663	0	0	0
	p	41985	0.5	4	158	34.80	1,790	80	0	0
	Sum	3	6.2	16	-	81.6	-	61	34	0
Hydroelectric Stations	p	14033	Point	-	-	0.95	1,390	No	No	Yes
	p	14034	Point	-	-	0.95	1,218	No	No	Yes
	p	14270	Point	-	-	0.50	174	No	No	Yes
	p	14269	Point	-	-	0.50	212	No	No	Yes
	p	13410	Point	-	-	0.77	141	No	No	Yes
	p	14467	Point	-	-	0.48	1,225	No	No	No
	p	14466	Point	-	-	0.48	1,338	No	No	No
	e	14920	Point	-	-	0.5	141	No	No	Yes
	e	14943	Point	-	-	0.5	140	No	No	Yes
	Sum	9	Point	-	-	5.6	-	-	-	7

p: production permit (the project should obtain approval of environmental terms before getting a construction permit and then operation permit), **e:** under evaluation (the project has not yet entered the production permit). **N:** number of wind turbines. **Rotor length** refers to the diameter of wind turbine rotors (m)

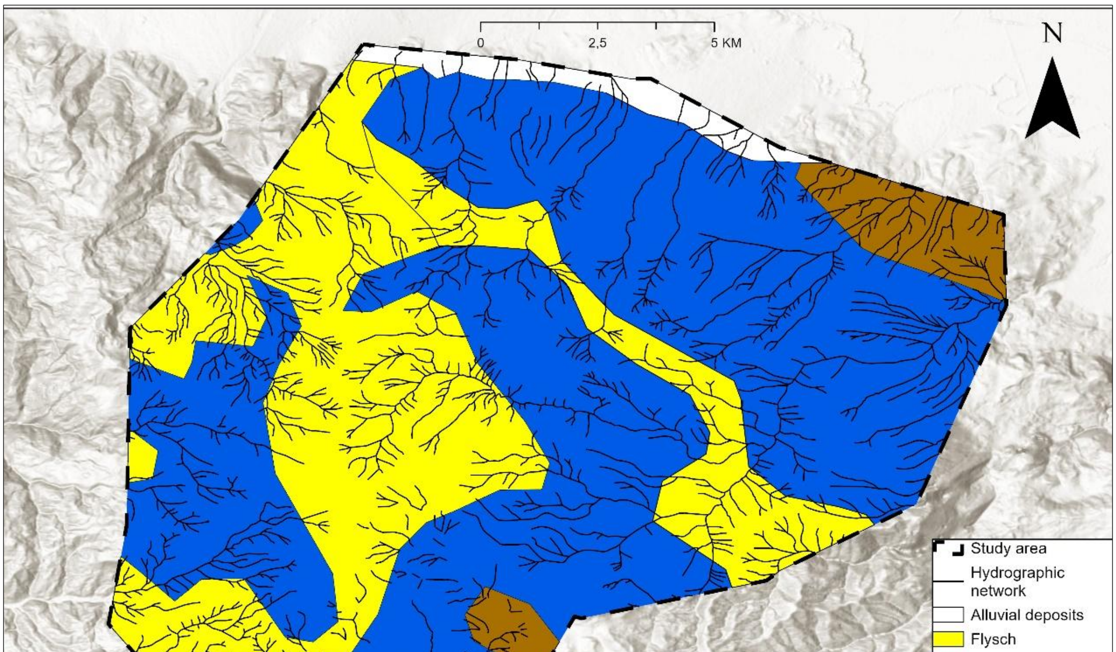

Figure 3A.1 Geological bedrock and hydrographic network in the study area of Mt. Oiti

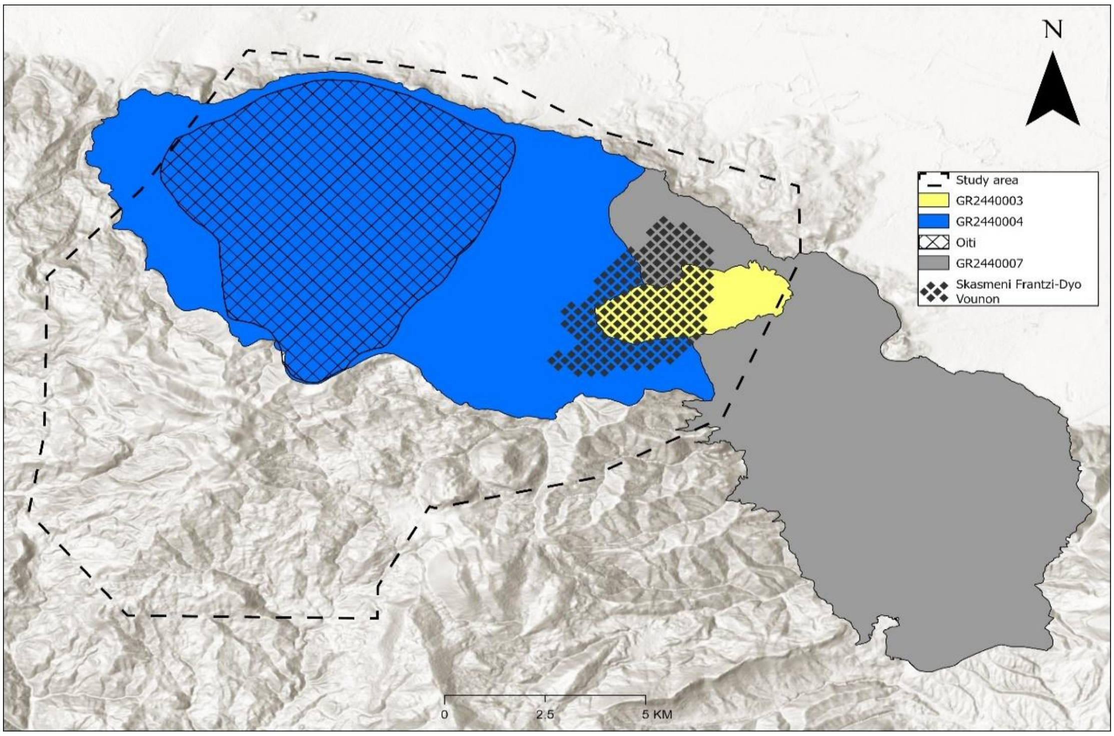

Fig. 3A.2 Sites of the Natura 2000 network overlapping with the study area of Mt. Oiti

GR2440003: "Farangi Gorgopotamou". Area: 5.3 km^2. Protected area category: Natura 2000 site: Special Area of Conservation (SPC). WDPA ID: 555527069

GR2440004: "Ethnikos Drymos Oitis". Area: 71.2 km^2. Protected area category: Natura 2000 site: Special Area of Conservation (SPC). WDPA ID: 555527070

Oiti: Area: 34.7 km^2. Protected area category: included in the Natura 2000 site GR2440004. WDPA ID: 2487. IUCN category: II (National Park)

GR2440007: "Ethnikos Drymos Oitis-Koilada Asopou". Area: 132.1 km^2. Natura 2000 type: Special Protection Area (SPA). WDPA ID: 555539707. IUCN category: none

Skasmeni Frantzi -Dyo Vounon: Area: 8.5 km^2. Protected area category: Wildlife refuge. WDPA ID: 341703. IUCN category: IV (Habitat/Species Management Area)

WDPA: World Database on Protected Areas (Protected Planet, 2025), IUCN categories according to (Dudley, 2008)

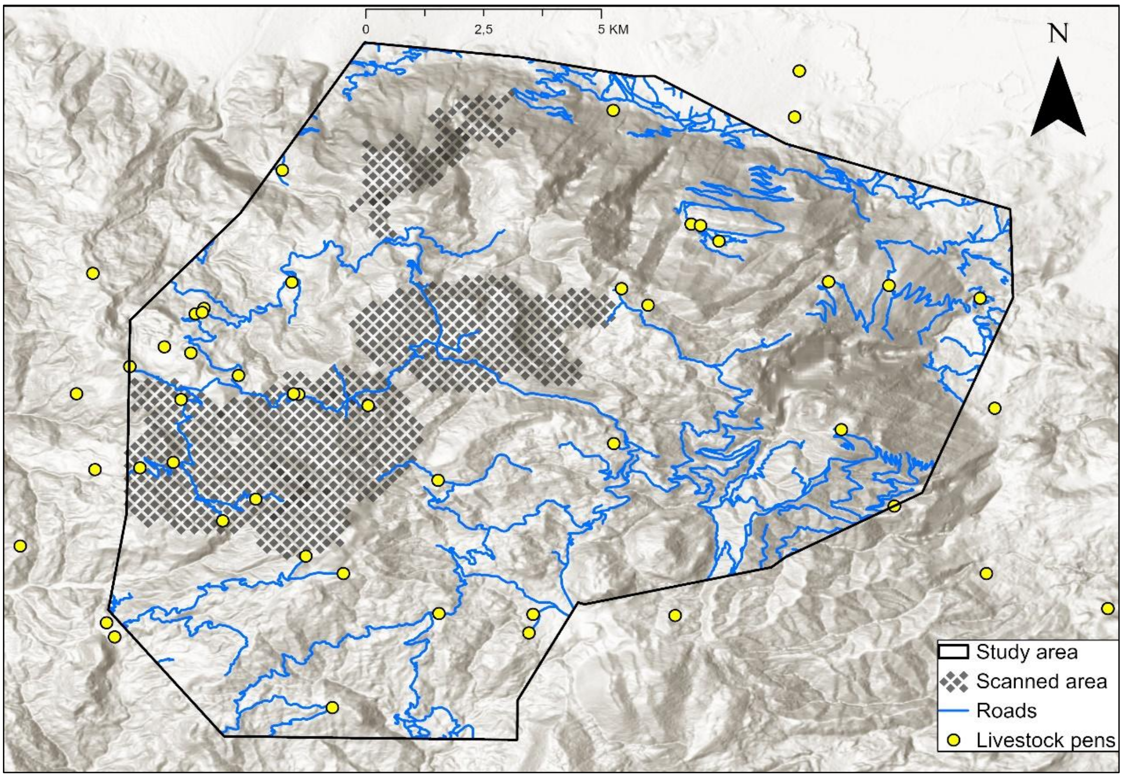

Fig. 3A.3 Scanned area for chamois surveys (2023), road network and livestock pens in the study area of Mt. Oiti

Chapter 4. Home range and habitat selection of chamois: a systematic review and meta-analysis

Published in *Mammal Review*

Papakostas, K., Chirichella, R., Apollonio, M., & Kati, V. (2026). Home Range and Habitat Selection of Chamois: A Systematic Review and Meta-Analysis. *Mammal Review*, 56(1), e70023. https://doi.org/10.1111/mam.70023

Abstract

1. Introduction: Chamois (*Rupicapra* spp.) are widely distributed across Europe and parts of Asia (ten subspecies). Studies on their distribution and habitat selection account for less than 10% of the literature on the genus, and existing research disproportionately focuses on the Alpine chamois (*R. r. rupicapra*).
2. Aims: We explored the chamois home range patterns and habitat selection drivers, trends in methodological data collection and analysis tools, and research gaps.
3. Methods: We conducted a systematic search (PRISMA guideline) and a meta-analysis of the peer-reviewed, English-language articles that reported quantitative data on home range size or habitat selection, comprising 22 studies spanning 16 study areas.
4. Results and Discussion: Knowledge stemmed mainly (68% of studies) from the Alpine subspecies. Seven subspecies remain understudied (0-1 study each). Telemetry and field observations were the primary field methods in home range and habitat selection studies, respectively. Annual individual home ranges were small but varied greatly (0.04-4.94 km^2), depending on sex (larger in males), dispersal behavior (larger in migrating males), and season. Habitat selection analysis (24 factors tested; 452 cases) revealed that topography (elevation, slope, escape terrain) and human disturbance (hunting, infrastructure, hiking trails, livestock) influenced chamois habitat selection. Rocky, grassland and forest habitat use were season-dependent, and snow-covered areas were generally avoided.
5. Recommendations: We highlight the need for further research on underrepresented and threatened subspecies, as well as on the chamois' responses to human disturbance and climatic variables, to better inform conservation management under global change.

Keywords

Rupicapra; Habitat preferences; Space use; Mountain ungulate

Introduction

Effective conservation of wildlife populations primarily depends on appropriate management, regulation enforcement, stakeholder engagement and control of direct human pressures such as poaching, hunting practices, and habitat alteration. Within this broader management framework (Nichols et al., 2024), , ecological knowledge on how animals use space can provide valuable context to support conservation and management decisions. Home range and habitat selection are interrelated ecological concepts crucial for understanding animal behavior and conservation planning. Home range refers to the area an animal uses for its regular activities, including foraging, mating, and shelter varying across species due to ecological and biological factors (Ofstad et al., 2016; Seigle-Ferrand et al., 2021). Research on home range contributes to our understanding of species distribution, habitat selection, predator-prey dynamics, community structure, and disease transmission (Börger et al., 2008). Habitat selection involves the specific environmental features that animals prefer within their home ranges relative to their availability (Northrup et al., 2022). Understanding the species-habitat relationships can provide insights into the potential impacts of climate and land-use change (Sohl, 2014), support the design and effectiveness of protected areas (Guisan et al., 2013), and help assess disease dynamics (Tardy et al., 2014), human disturbance (Ripari et al., 2022), and interspecific competition (Torretta et al., 2021).

This study focuses on the chamois (*Rupicapra* sp.), an iconic mountain ungulate found at variable elevations throughout Central, Western and Southern Europe, the Near East and in New Zealand, where chamois have existed since their introduction in 1907 and 1914 (Corlatti et al., 2022b). The genus *Rupicapra* includes two species, *Rupicapra rupicapra* (Northern chamois), comprising seven subspecies (*cartusiana*, *rupicapra*, *balcanica*, *tatrica*, *carpatica*, *caucasica* and *asiatica*) and *Rupicapra pyrenaica* (Southern chamois) comprising three subspecies (*ornata*, *parva* and *pyrenaica*) (Corlatti et al., 2022b). While both species are classified as Least Concern (LC) by the IUCN Red List of Threatened Species, five out of the 10 subspecies are threatened (Endangered: *R. r. asiatica*, *R. r. tatrica*, ; Vulnerable: *R. r. cartusiana*, *R. r. caucasica*, *R. p. ornata*), while even some populations of the most abundant subspecies (*R. r. rupicapra, R. p. parva* and *R. p. pyrenaica*) have started to decline (Anderwald et al., 2021a; Herrero et al., 2024). The most common threats to chamois include poaching and overhunting, human disturbance, habitat loss and degradation, climate change, competition with livestock, diseases, and hybridization among subspecies (Corlatti et al., 2022c).

Although research on chamois has increased substantially between 1980 and 2020, greatly improving our understanding of the species' biology and ecology, most of the studies have focused primarily on the Alps and the Alpine subspecies (Corlatti et al., 2022c). During this period, research on habitat selection, movement, and distribution of the species has accounted for less than 10% of the total research (Corlatti et al., 2022c). In this review, we aimed to provide a systematic overview and meta-analysis of the chamois' home range size and habitat selection, with the objectives of evaluating existing knowledge, identifying critical gaps, highlighting key environmental factors influencing the species' ecology, and offering guidance for future research and conservation efforts. We address the following questions: (a) How well are different chamois species and subspecies studied regarding their home range and habitat selection? (b) What are the research trends concerning the methodological tools used for data collection and analysis of chamois habitat use over the last four decades? (c) What are the home range and core area patterns of the species? (d) What are the primary factors shaping the habitat selection of the species according to different methodological analyses?

Methods

We conducted the systematic review in accordance with the PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) guidelines (Page et al., 2021) for record selection (**Fig. 4.1**). We performed all analyses using R (version 4.4.3) (R Core Team, 2023).

Data collection

We conducted a literature search in Scopus up to 1 March 2025, using specific search terms in the title, abstract, and keywords. For species identification, we used the terms "*Rupicapra*", "chamois", or "isard", and for habitat selection and home range studies, we included "habitat selection", "habitat use", "habitat preferences", "ecological niche", "home range", "distribution", and "core area". The search was limited to peer-reviewed journal articles published in English and returned a total of 193 documents.

After screening the titles and abstracts, we excluded 161 documents that were not relevant to the species or the study's focus. We further excluded four studies that lacked data on average or individual home range size, six descriptive studies that conducted no statistical data treatment, and one study for which the full text was not accessible. This initial screening resulted in 21 eligible studies.

After selecting these studies, we also checked their reference lists and identified one additional relevant study that did not appear in the Scopus search. The final dataset comprised 22 studies: eight focused on home range, 11 on habitat selection or habitat use, and three addressed both topics **(Fig. 4.1).**

Data analysis

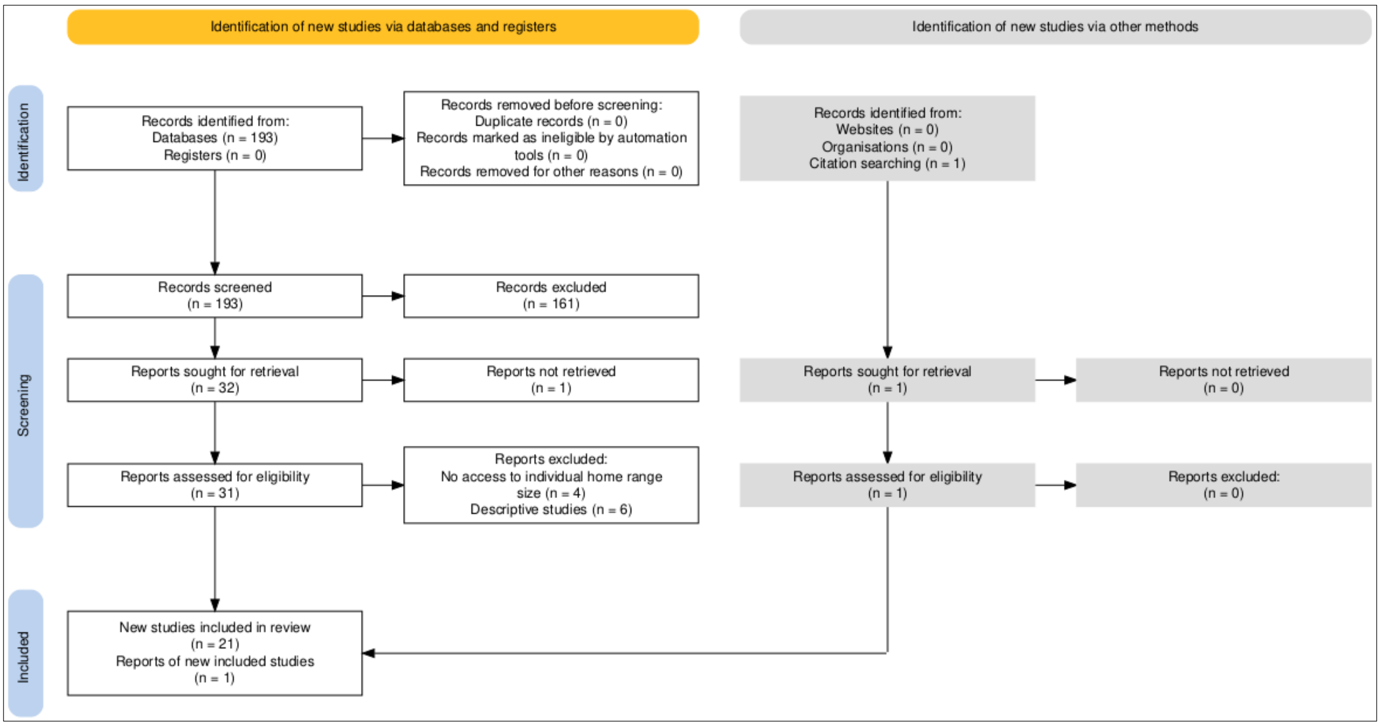

Fig. 4.1 PRISMA flow diagram according to the PRISMA statement by (Page et al., 2021).

Datasets

We reviewed the literature and compiled a database comprising three interlinked datasets, each associated with a corresponding paper code (**Table S1**). We classified each study as either a "Home range" **(Table S2)** or a "Habitat selection" study **(Table S3)**. We then categorized the studies according to their data collection methods, grouping them into three categories. Field observations included studies that collected chamois observations from fieldwork. The telemetry category comprised studies using GPS or VHF-collared animals. The combination category included studies that employed field observations in combination with telemetry (two studies) or other data sources (one study of archeozoological data). We also categorized the studies according to two data analysis methods: statistics and models. The first category included all studies that employed descriptive statistics or basic statistical tests. The second category comprised studies that employed modelling techniques such as Kernel Density Estimates (KDE), Generalized Linear Models (GLMs), Ecological Niche Factor Analysis (ENFA), and other similar approaches.

The "Studies" dataset **(Table S1)** included general information on the papers, such as citation details, country of study, species and subspecies of chamois examined, data collection and analysis methods, and geographic coordinates of the study areas. Coordinates were either directly provided by the authors or estimated as the approximate centroid of the study area. In cases where the research spanned more than one country (two instances), we only reported the country names. The "Home range" dataset **(Table S2)** included all studies related to this topic. It included information on the chamois species, year(s), season/period and method of data collection, demographic information of the population studied (sex, age, and presence of young), resident or migrant status, and the total number of individuals studied. The dataset also included the data analysis method employed, as well as the mean size and standard deviation (in square kilometers) of the home range and its associated core area. We distinguished between studies that calculated individual home ranges and those that estimated population-level ranges, such as kernel density estimation (KDE), based on all field observations within a defined study area. In one study encompassing two study areas, we noted the locality, i.e., the name of the study area as referred to in the paper.
The habitat selection dataset (**Table S3**) included the factors assessed in each study, using the original terminology employed by the authors, their description, the interaction between factors, the types of coefficients and values, the standard error (SE), the significance level, the nature of the impact (positive or negative), the interpretation of the impact and additional comments. To streamline our analysis, we grouped the variables into 30 subcategories and identified 24 habitat-related factors (excluding six not habitat-relevant subcategories). We further classified these into four broad categories: land cover, topography, disturbance, and climatic factors. We then considered four types of data analysis methods. (a) GLM-type studies included Generalized Linear Models (GLMs), Generalized Linear Mixed Models (GLMMs), Resource Selection Functions (RSFs), and multiple regression analyses. (b) ENFA-type studies used either ENFA or Mahalanobis Distances Factor Analysis (MADIFA). (c) Selection ratio studies employed indices such as Jacobs' Second Selection Index and the Manly Index. (d) Descriptive statistical approaches included methods like the two-tailed test.

Knowledge gaps and research trends

We employed descriptive statistics to explore knowledge gaps and research trends over time using the studies dataset (**Table S1**), focusing on the different chamois species and subspecies studied, as well as the data collection and analysis techniques employed. We visualized the study areas included in our database by creating a map using ArcGIS Pro (version 3.2.2).

Home range

Using the home range dataset (**Table S2**), we summarized home range sizes separately for males and females based on the values reported in each study. For each sex, we calculated descriptive statistics, including the mean and standard deviation, minimum, and maximum values, to provide an overview of the variation in home range size. We also reported results from three studies that distinguished between “resident” (males that occupy small and stable home ranges) and “migrant” (males that move between seasonal areas) males (Lovari et al., 2006; Nesti et al., 2010; Unterthiner et al., 2012).

Habitat selection

Using the habitat selection dataset (**Table S3**), we analyzed the results from GLM-type studies by conducting random-effects meta-analysis for each factor using the "metafor" R package (Viechtbauer, 2010). Effect sizes (β) were combined across studies, weighted by their inverse variance ($1/SE^2$). We quantified between-study heterogeneity using τ^2, which reflects the variance of true effects, and I^2, which captures the degree of overlap among confidence intervals. To assess the contribution of moderators, we calculated R^2 as an estimate of the proportion of heterogeneity explained (Borenstein et al., 2021; Nakagawa et al., 2023; Schwarzer, 2022). To assess contextual variation in habitat selection, we ran mixed-effects meta-regressions for all factors with significant pooled effects, including the season (annual, spring, summer, autumn, winter) and the analysis method (e.g., GLM) as moderators. We included moderators (season and method) in the meta-regression models only when sufficient data were available across levels for a given factor. In all meta-regression models, we treated "annual" as the reference category for the season and "GLM" as the reference for the analysis method. As such, intercept terms represent the estimated effect under these baseline conditions. We used Study ID as a random effect to account for multiple estimates per study. We created visualizations using the package "ggplot2" (Wickham, 2016).

To evaluate habitat selection from studies employing ENFA, we extracted marginality information for all environmental variables analyzed per study. ENFA predicts habitat selection based on the ecological distance between the mean habitat used by a species and the global habitat available in the study area. The marginality axis quantifies the degree to which the utilized habitat differs from the average available conditions, with positive or negative values indicating selection or avoidance, respectively (Hirzel et al., 2002). We classified each factor by its direction of marginality (M): positive (indicating selection), negative (indicating avoidance), or neutral. We considered marginality values ≤0.2 as neutral. To summarize findings across studies, we applied a vote-counting approach (Borenstein et al., 2021). For each factor, we calculated the number of positive, negative, and neutral outcomes across all ENFA studies. We also computed a simple selection score as the difference between positive and negative cases (positive-negative) to identify overall trends. This method allowed us to compare factor-level habitat preferences across studies without relying on raw model outputs, which are not always available in ENFA frameworks. While this approach does not account for effect size variance, it is a robust alternative when standardized coefficients are unavailable (Borenstein et al., 2021).

Selection ratio indices estimate selection strength relative to habitat availability but often lack variance estimates or consistent scaling across studies (Manly et al., 2002). For each factor, we classified the direction of selection as Positive (selected), Negative (avoided) and Neutral (no significant difference between use and availability, or index ≈ 1). We then applied a vote-counting approach, calculating the number of positive, negative, and neutral outcomes across all studies of selection ratios. Finally, we computed a selection score for each factor (positive-negative) to assess the consistency and strength of its effect across studies. One study assessed habitat selection using basic descriptive statistics and was excluded from the analysis.

Publication bias

We assessed potential publication bias (i.e., the increased likelihood that smaller studies are published if they report stronger effects) using contour-enhanced funnel plots, which depict the relationship between effect sizes (β) and their standard errors. These plots enable the visual identification of asymmetry and provide insight into whether any missing studies may be located in areas of statistical significance or non-significance (Schwarzer, 2022). To formally test for asymmetry, we conducted both Egger's regression test by fitting a meta-regression model with the standard error as a predictor of effect size (Egger et al., 1997) and trim-and-fill analysis (Duval & and Tweedie, 2000). We conducted this analysis for all habitat-related factors with at least 10 effect sizes, specifically slope, elevation, and aspect (south), using the "metafor" package in R (Viechtbauer, 2010). Egger's test indicated significant funnel plot asymmetry for all three variables: slope ($p < 0.0001$), elevation ($p = 0.037$), and aspect (south) ($p = 0.026$). However, the trim-and-fill method did not impute any missing studies for any of these factors, suggesting that the observed asymmetry may not be due to unpublished small or negative studies. These findings suggest that although small-study effects may be present, they do not substantially alter the main conclusions regarding the significant predictors.

Results

We found that the 22 studies included in this review encompassed 16 distinct study areas across eight different countries (**Table S1**). Most of these study areas were in central and southern Europe, with one study conducted in New Zealand (**Fig. 4.2**).

Knowledge gaps and research trends

Most of the 22 studies focused on the Northern chamois (*Rupicapra rupicapra*: 19 studies: 86%) and fewer on the Southern chamois (*Rupicapra pyrenaica:* three studies: 14%) (**Fig. 4.3**). The most

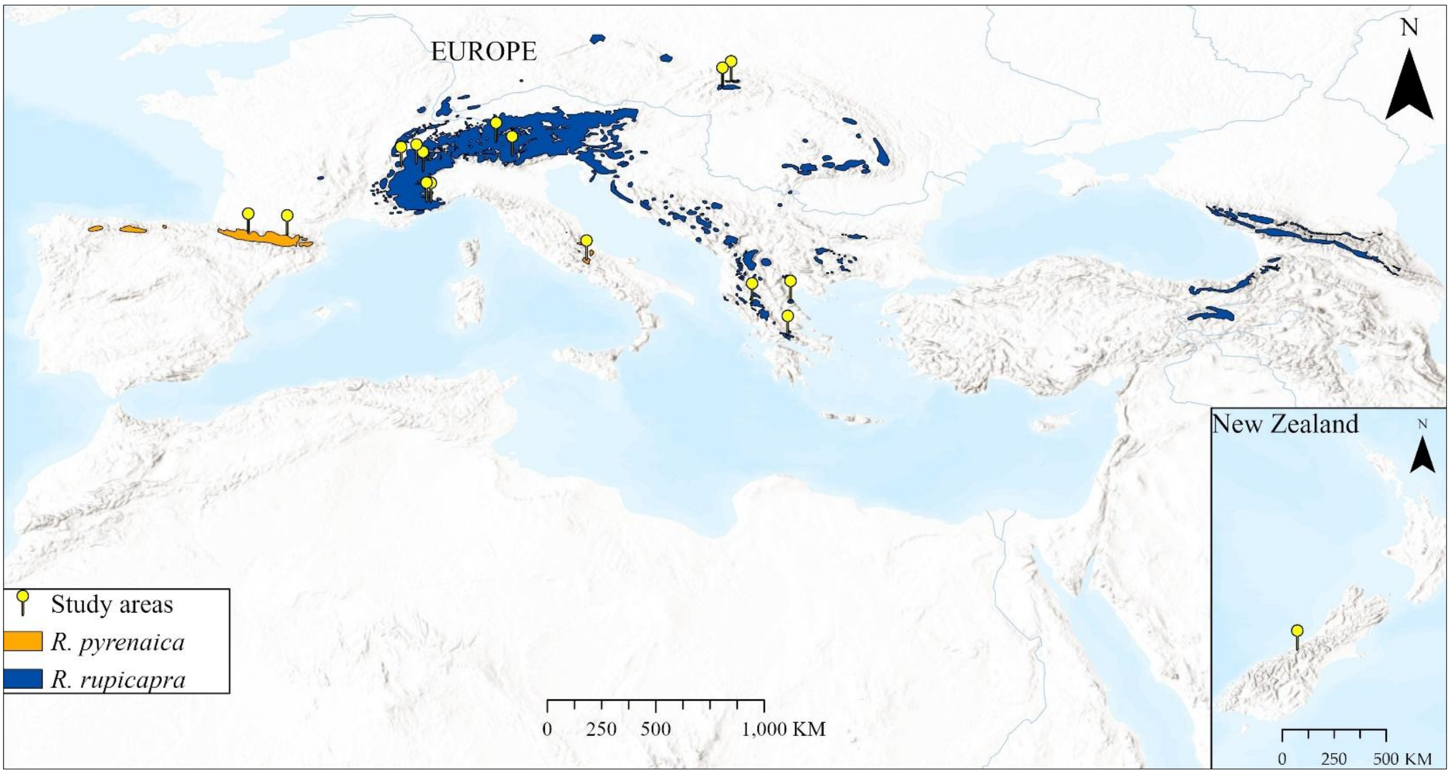

Fig. 4.2 Geographic distribution of study areas included in the review across the IUCN-defined range of the two chamois species (Anderwald et al., 2021a).

well-studied subspecies were the Alpine chamois *R. r. rupicapra* (68% of studies), followed by the Balkan chamois *R. r. balcanica* (14%) and the Pyrenean chamois *R. p. pyrenaica* (9%). Two subspecies were poorly studied, with only one study each: *R. r. tatrica* and *R. p. ornata* (4% of studies). Five subspecies are not studied at all in terms of home range and habitat selection: *R. r. asiatica*., *R. r. caucasica*, *R. r. cartusiana*, *R. r. carpatica* and *R. p. parva* (**Fig. 4.3**).

We found a fluctuating trend in the number of home range studies, peaking in the previous decade and an increasing trend in the number habitat selection studies (**Fig. 4.4**). In home range studies, telemetry was the primary data collection method employed, followed by field observations. Modelling was the exclusive method used for data analysis, regardless of the data collection approach (**Fig. 4.4, Table S1**). In habitat selection studies, field observations were the predominant

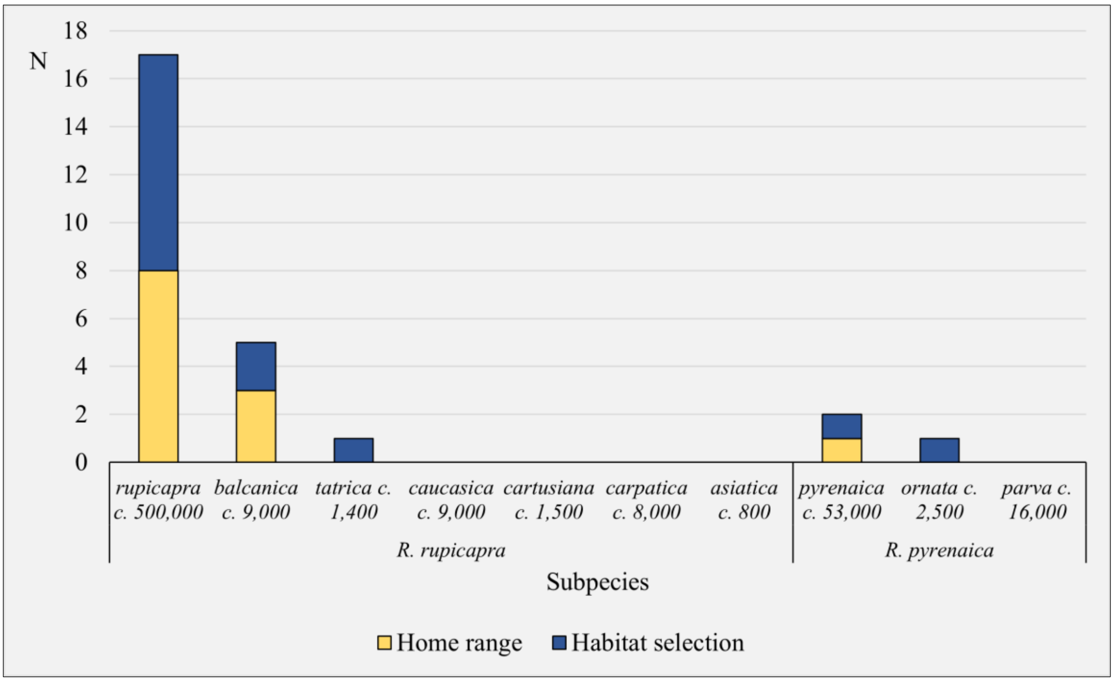

Fig. 4.3 Knowledge gaps in chamois research. Number of studies (N) investigating home range (yellow) and habitat selection (blue) across the ten chamois subspecies. Subspecies are grouped by species (*Rupicapra rupicapra* and *Rupicapra pyrenaica*), with approximate global population estimates shown below each name (c = circa) (Corlatti et al., 2022b).

method for data collection, while modelling was the most popular method for data analysis (**Fig. 4.4**).

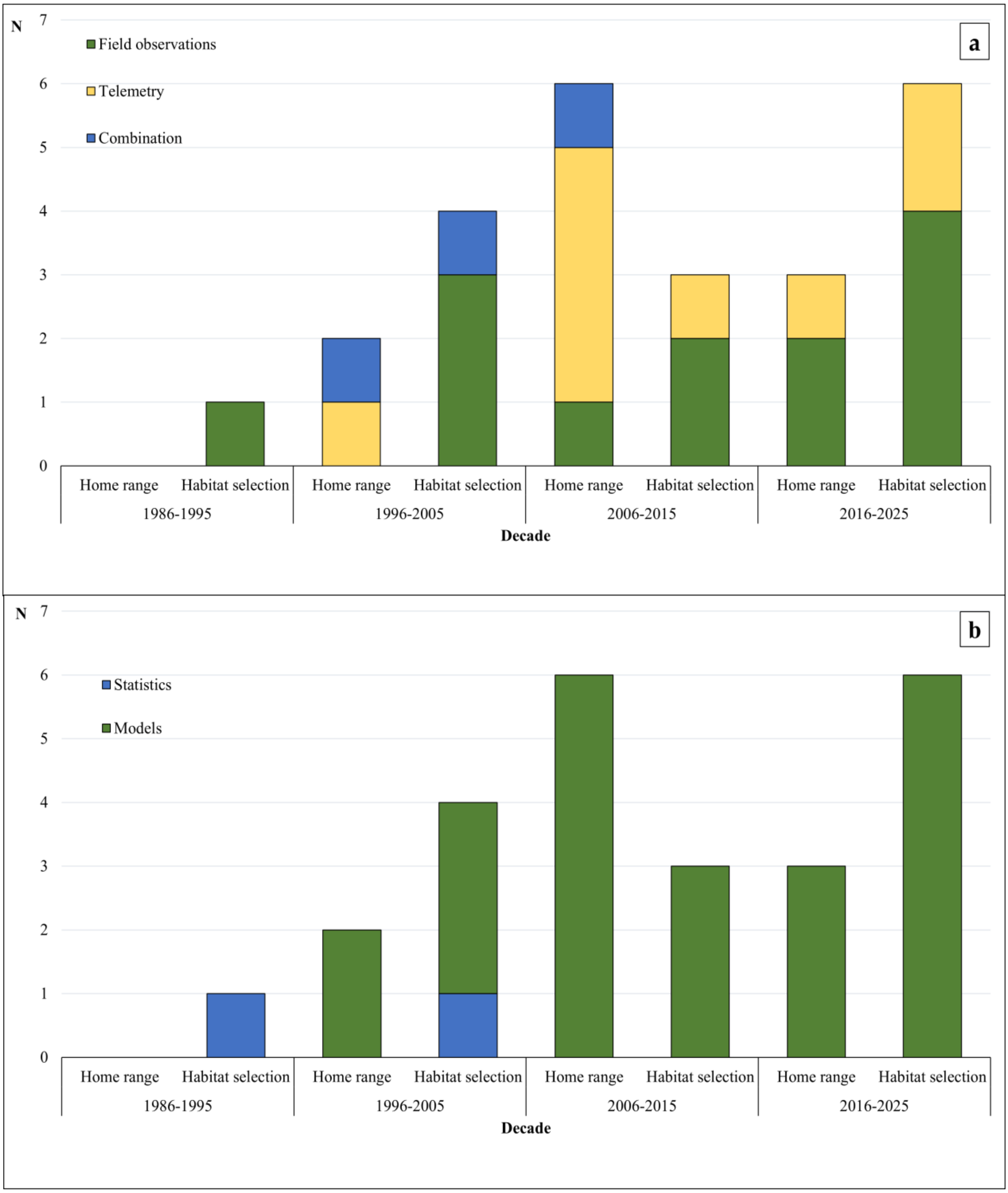

Fig. 4.4 Research trends in methodological approaches used in chamois home range and habitat selection studies over the past four decades (based on 22 studies reviewed): (a) Field methods employed for data collection, categorized as field observations, telemetry, and combined approaches and (b) Data analysis methods used, grouped into statistical and modelling approaches.

Home range

Home range sizes reported for females ranged from 0.64 to 0.87 km^2 (mean = 0.72 ± 0.10 km^2), while male home ranges ranged from 0.04 to 4.94 km^2 (mean = 1.21 ± 1.34 km^2) (**Table 4.1**). Core area sizes were also slightly larger in males (0.03-0.57 km^2; mean = 0.18 ± 0.19 km^2) than in females (0.12-0.17 km^2; mean = 0.15 ± 0.02 km^2). When considering only the three studies that focused on migrant and resident males, migrant males demonstrated larger home ranges (mean = 3.05 ± 2.66 km^2) and core areas (mean = 0.49 ± 0.49 km^2) compared to resident males (mean = 0.44 ± 0.19 km^2 and mean = 0.06 ± 0.02 km^2 respectively). Three studies examined population home ranges, showing almost two-fold variation in population home range areas (**Table 4.1**).

Table 4.1 Summary of the home range and core area in the chamois *Rupicapra* spp. Mean (± standard deviation), minimum and maximum values of annual home range and core areas for females (F), males (M), both sexes (M+F), and the whole population (P), noting the number of studies (N) and the number of individuals considered (i). Annual population ranges and core ranges are presented separately.

		Individual home ranges				
		Annual Home Range (km^2)			**Annual Core Area (km^2)**	
Sex	**N (i)**	**Mean (SD)**	**min-max**	**N (i)**	**Mean**	**min-max**
F	3 (64)	0.72 (±0.1)	0.64-0.87	2 (14)	0.15 (±0.02)	0.12-0.17
M	5 (65)	1.21 (±1.34)	0.04-4.94	3 (44)	0.18 (±0.19)	0.03-0.57
M+F	1 (29)	0.61 (±0.42)	-	1 (29)	0.08 (±0.7)	-
		Population home range				
	N	**Annual Range**	**min-max**	**N**	**Annual Core Area**	**min-max**
P	3	64.06 (±50.08)	16.75 -201.2	3	24.95 (±15.55)	4.67-51.8

Habitat selection

The habitat selection database (**Table S3**) included 14 studies with 452 cases corresponding to 24 factors that had been used in studies of chamois habitat selection. In most cases (393, 87%), a statistically significant ecological preference was recorded. The most well-studied category referred to land cover factors (13 studies; 203 cases), followed by topography (13 studies; 162 cases), while disturbance (six studies; 42 cases) and climatic factors (four studies; 26 cases) have been less often tested in habitat selection studies (**Table S3**).

GLM-type studies

The analysis involved seven GLM-type studies (188 cases) for chamois and seven environmental factors across at least three cases (**Table S3**). Among these, only three factors showed statistically significant average effects (intercept values; $p < 0.05$) (**Fig. 4.5**). Chamois selected steeper slopes (five studies), with a significant pooled effect under annual conditions, as determined by GLM analysis ($\beta = 2.60$, 95% Confidence Interval (CI): [0.39, 4.80], $p = 0.021$). Moderator terms for season and method were not statistically significant, indicating that the strength of slope selection did not vary substantially across seasons or analytical approaches.

Snow and ice (three studies) were generally avoided, with a significant negative pooled effect under annual conditions (β = -2.32, 95% CI: [-2.86, -1.78], $p < 0.0001$). In the winter models, use of snow and ice was higher compared to the annual average (β = +2.34, 95% CI: [1.81, 2.88], $p < 0.0001$). Forested habitats (three studies) were positively selected, but their effect was small (β = 0.12, 95% CI: [0.03, 0.21], $p = 0.008$).

The remaining factors (elevation, aspect-south, grassland, and competition) did not have consistent effects across studies. The results for most factors differed widely from one study to another ($I^2 > 90\%$). Elevation was the only case where this variation could be partly explained: differences in season and method accounted for about 43% of it. For the other factors, season and method explained almost none of the variation ($R^2 \leq 1.2\%$).

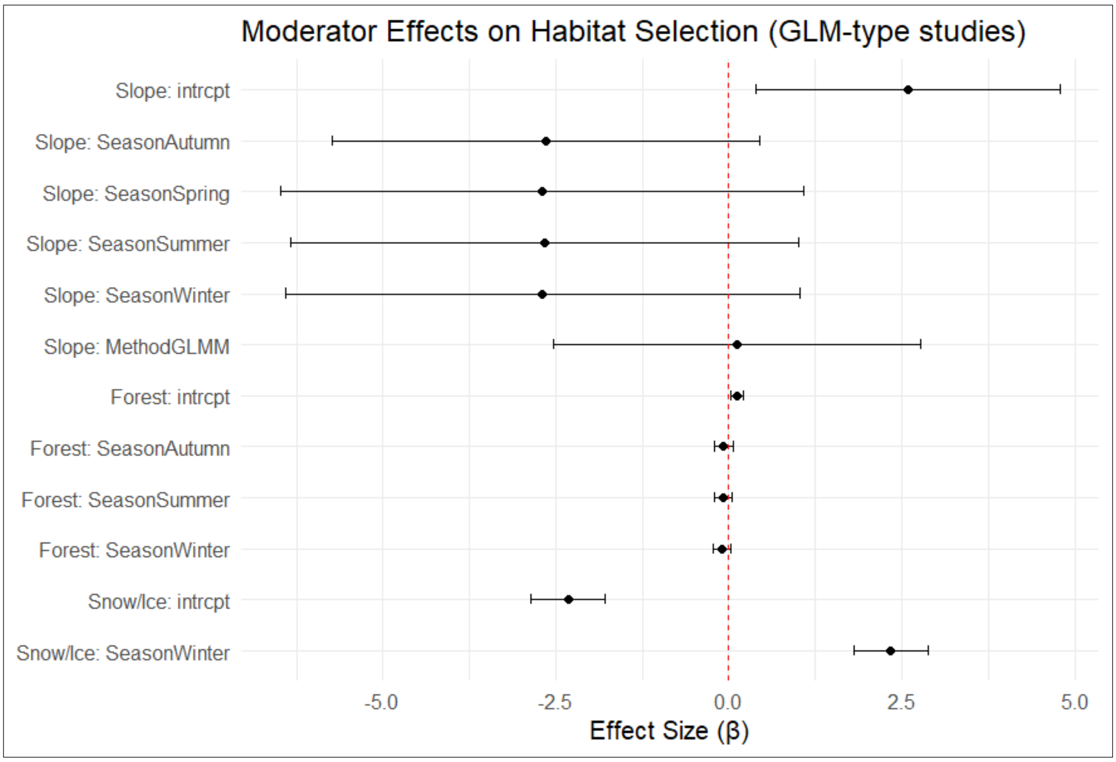

Fig. 4.5 Moderator effects on chamois habitat selection based on GLM-type studies. Each point represents an estimated effect size (β) with 95% confidence intervals for a given moderator level. The red dashed line indicates no effect (β = 0). Intercepts (intrcpt) refer to baseline categories for each variable.

ENFA-type studies

Results were referred to four ENFA-type studies, which included 158 cases of 21 different factors. Topography and then land cover influenced most habitat selection patterns (**Fig. 4.6a**). Elevation showed the highest cumulative positive signal among all factors (score = +11), followed by slope, north aspect and escape terrain. In contrast, southern aspects were consistently avoided, and other variables, such as terrain ruggedness and western aspect showed neutral effects.

Within land cover factors, rocky habitats showed strong and consistent selection. Grasslands were generally favored (six positives, two negatives; score = +4), while forests produced mixed results (three positive, three negative, 12 neutral). NDVI (Normalized Difference Vegetation Index) and bushland showed weaker selection scores, while cultivated land (agricultural areas) was mainly neutral.

Disturbance variables were related to negative scores and, consequently, avoidance patterns of chamois, except hiking trails. Hunting was the most negatively selected factor (six negative out of six cases), followed by infrastructure (15 negative and one neutral out of the 16 cases) and competition with other herbivores (one negative case). Chamois selected areas near hiking trails (four positive and one negative out of five cases). Climatic factors had weaker and less consistent associations, resulting in zero scores, except for humidity (one negative, four neutral out of the five cases) (**Fig. 4.6a**).

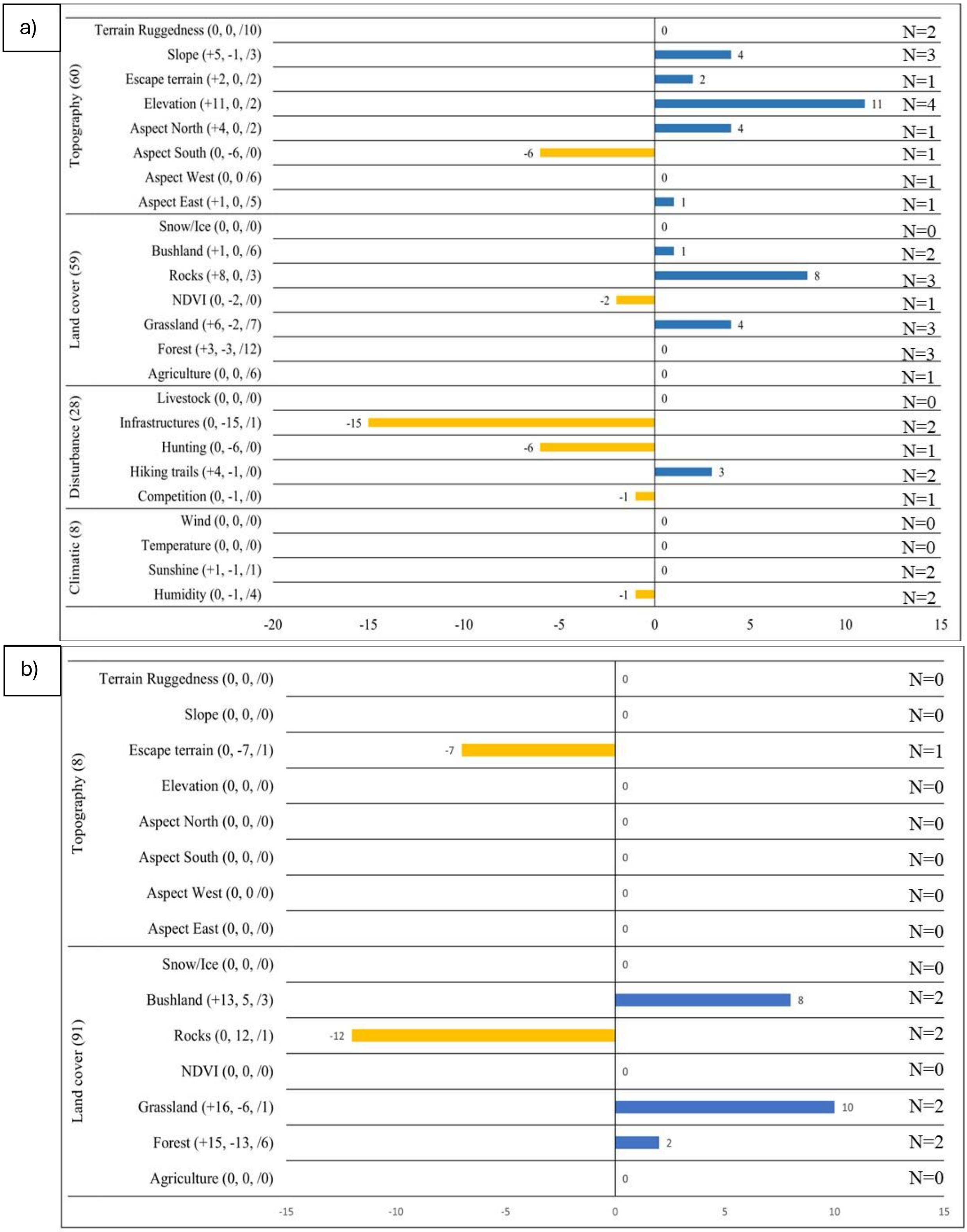

Figure 4.6 Summary of habitat selection factors affecting chamois, based on (a) ENFA studies and (b) selection ratio studies. Bars represent the selection score for each factor, calculated as the difference between the number of positive and negative cases. Numbers in parentheses beside each factor indicate the distribution of results across studies in the order: positive (+), negative (−), and neutral (/). The total number of cases per factor category (topography, land cover, disturbance, climate) is provided in parentheses. N is the number of studies for each factor.

Selection ratio studies

Results referred to two selection ratio studies, including 99 cases of five different factor subcategories (Table S3). From the topographic variables, only the escape terrain was assessed, showing negative selection (seven negative, one neutral case) (**Fig. 4.6b**). From the land cover types assessed, grasslands yielded the highest positive cumulative selection score (+10), followed by bushlands (+8) and forests (+2), while rocky habitats were avoided (-12). No climatic or disturbance variables were assessed using this method.

The single study that assessed habitat selection using basic descriptive statistics found that chamois preferred steep slopes (≥ 65°) sheltered from the wind during the period defined by the authors as "cold" (January-June), and more exposed slopes during the period defined as 'warm' (July-December). It also reported that chamois used alpine meadows more frequently than forests during the warm period, while the opposite pattern was observed during the cold period.

Discussion

Knowledge gaps and research trends

Our results showed that most studies (86%) focused on the Northern chamois, and particularly the Alpine chamois (68%; 15 studies). By contrast, only four subspecies have been studied (seven studies in total), with five subspecies not represented at all in chamois habitat-use studies (**Fig. 4.3**). Therefore, most of the existing knowledge regarding home range and habitat preferences is derived from a single subspecies and primarily from one mountain range, the Alps. On one hand, this knowledge gain has contributed to drafting the action plans for less well-studied species and their habitats, such as the Balkan chamois in Greece (Papaioannou, 2021) and Bulgaria (Avramov & Valchev, 2010), the Apennine chamois in Italy (Dupré et al., 2001), and the Tatra chamois in Slovakia (ŠOPSR/TANAP, 2002). On the other hand, to address the various threats faced by chamois (Corlatti et al., 2022c), it is crucial to expand research efforts for delineating the current distribution range and understand the chamois ecological needs at the subspecies level, prioritizing research for the least studied subspecies that often are of conservation concern (**Fig. 4.3**).

We also found a growing research trend on chamois habitat selection over the last decades, highlighting the increasing need to understand the ecological preferences of the species. Field observations were the predominant method for data collection in habitat selection studies, and telemetry was more commonly utilized to study home ranges (**Fig. 4.4**). Telemetry has been employed primarily in Italy, followed by Switzerland and France, whereas field observations have been conducted in all countries (**Table S1**). Given the advantages of telemetry studies (Hebblewhite & Haydon, 2010), we stress the need to promote its wider adoption, particularly in countries with understudied or declining chamois populations. This requires not only targeted knowledge exchange but also efforts to overcome financial and technical barriers that limit access to telemetry tools and expertise. Supporting local researchers through funding, collaboration, and training initiatives is critical for advancing chamois research and conservation across their full range.

Home range

Our review showed substantial variability in individual home ranges (minimum-maximum home range values) across the eight studies considered (**Table 4.1**). The area utilized by each chamois is case-specific, and various local factors can influence it, explaining the variability in the home range. These factors include food quality and quantity (Boschi & Nievergelt, 2003; Nesti et al., 2010), energy requirements, and territorial status (Lovari et al., 2006; Unterthiner et al., 2012; von Hardenberg et al., 2000). The home range estimation depends on the analytical methods and sample sizes involved, further explaining the great variability found (Laver & Kelly, 2008). In any case, our review showed that chamois display smaller annual home ranges (0.61-1.21 km^2; **Table 4.1**) compared to other ungulates, such as the red deer (*Cervus elaphus*) (2-35 km^2) (Mattioli et al., 2022), the mouflon (*Ovis gmelini*) (2-17 km^2) (Garel et al., 2022) and the ibex (*Capra ibex*) (6.1-22.6 km^2) (Valldeperes et al., 2024).

Sex, dispersal behavior and predator presence can influence home ranges. According to the eight studies reviewed, males tended to have slightly larger individual home ranges than females (**Table 4.1**), though the inverse pattern has also been reported once (Boschi & Nievergelt, 2003). Males exhibit greater dispersal abilities to avoid inbreeding. However, females are more philopatric, remaining in areas where they have established knowledge of local resources, which helps ensure the survival of their offspring (Corlatti et al., 2022b; Loison et al., 1999). Furthermore, three studies on alpine chamois confirmed that migrant males occupy larger home ranges and core areas than resident males, likely as they search for new territories and mating opportunities. On the other hand, resident males tended to remain at lower altitudes with relatively small home ranges throughout the year, defending their territories and enhancing reproductive success (Lovari et al., 2006; Nesti et al., 2010; Unterthiner et al., 2012). However, dispersal status should not be confused with territoriality, as territorial males are not necessarily residents, and residents are not necessarily territorial (Cotza et al., 2023). Predator presence can also influence the space use pattern. In a protected area with minimal human disturbance and no predators (Swiss National Park), female chamois with offspring utilized larger areas than those without young to improve feeding conditions (Boschi & Nievergelt, 2003). This pattern may be reversed in areas with higher predator presence and human disturbance, where females with young might stay closer to escape terrain for protection, similar to behaviors observed in other ungulates (Aycrigg et al., 2021; Bon et al., 1995; Hamel & Côté, 2007).

Seasonality is another major factor influencing both individual home ranges and seasonal population ranges. Most chamois populations exhibit smaller individual and population ranges during the cold period in Europe (Crampe et al., 2007; Kati et al., 2020; Krofel et al., 2013; Lovari et al., 2006; Nesti et al., 2010) and New Zealand (Clarke & Henderson, 1984), as winter harshness is the primary stress factor limiting available resources. In warmer regions of Europe, however, this pattern is reversed in population studies (Mediterranean seasonal range pattern), with summer heat serving as the main stressor for the species in drier mountains (Papaioannou et al., 2015; Papakostas et al., 2025b).

Currently, knowledge regarding the species' home range is based on only three subspecies across four countries. Therefore, home range size and patterns may differ in other subspecies and habitats where chamois exist. We recommend further research to investigate the remaining six understudied subspecies in Europe and Asia.

Habitat selection

According to the review results, land cover and topography were the most well-studied categories. Although disturbance and climatic factors may influence chamois habitat selection, their effects remain poorly understood due to limited investigation.

Topography

Topographic variables consistently influenced chamois habitat selection across all analytical methods. The slope was examined in nine studies, and it was generally found to be positively selected (in both GLM-type and ENFA-type studies). Our meta-analysis of the five GLM-type studies indicated a significant annual effect and a non-significant seasonal interaction. However, as these findings are based on only five studies, strong conclusions cannot be drawn. This preference likely reflects the chamois' morphological and behavioral adaptations to steep, rugged environments that provide both forage and escape terrain. Steep slopes are critical escape terrain for chamois and represent one of the most important factors influencing their habitat selection (Anderwald et al., 2024; Lovari & Cosentino, 1986). Although our review revealed no seasonal variation in the selection of slope, some studies have shown that chamois exhibit a preference for steeper slopes during colder seasons compared to warmer months (Babaev et al., 2016; Corlatti et al., 2021; Papaioannou et al., 2015).

Elevation has been well examined, showing a positive association with habitat use. Although elevation did not show a statistically significant average effect across the five GLM-type studies, the moderators explained a substantial portion of the between-study heterogeneity (R^2 = 43%), suggesting that the role of elevation in habitat selection is highly dependent on season. In four ENFA-type studies, 11 out of 13 cases indicated selection for higher elevations, particularly during summer. This is consistent with the species' ecology, as chamois typically occupy higher-elevation grasslands from late spring to autumn, up to 3,000 m above the tree line, and lower elevations in forests during winter. However, some populations remain in forests throughout the year (Corlatti et al., 2022b). During winter, the preference for lower elevations intensifies with increased precipitation and wind speed (Anderwald et al., 2024). The use of elevation zones also depends on competition with livestock, with chamois retreating to higher altitudes due to the presence of livestock (Mason et al., 2014b) or colonizing abandoned livestock pastures at lower elevations (Ciach & Pęksa, 2019).

Aspect has been examined in five studies (four GLM-type and one ENFA-type study). It had no significant effect in habitat selection according to the GLM-type studies. However, in one ENFA-type study (Kati et al., 2020), north-facing aspects were selected in most cases, and south-facing slopes mainly were avoided, indicating the species' capacity to cope with cold, snowy environments. Aspect appears not to have a major effect on habitat selection, as the species can select different aspects depending on local topography and climate, the season, and the availability of adequate habitats across various aspects.

Land cover

Land cover factors revealed mixed patterns of selection across 13 studies, including snow/ice cover, forest cover, rocks, grasslands, and bushlands. The results of the three GLM-type studies indicated a significant overall annual avoidance pattern of snow/ice covered areas (**Fig. 4.5**). In winter models, use of these habitats was higher compared to annual models, suggesting that the effect is driven more by availability than by active selection. Chamois can avoid glacier-covered areas (Baumann et al., 2005), not being substantially affected by snow cover (Forsyth, 2000), or retreat to forested areas (interaction with tree cover density) in response to the first snowfall and overwinter there in snow-covered areas (Anderwald et al., 2024) (**Fig. 4.5**).

Forested areas also exhibited highly variable selection patterns. Chamois selected forested areas, but the effect size was weak in GLM-type studies (three studies). ENFA-based studies (three studies) revealed no consistent trend, with both positive and negative associations reported (score 0). In contrast, the two selection ratio studies indicated a rather positive association (score +2), which also included neutral or negative cases. These mixed results likely reflect substantial seasonal and regional variation in forest use, potentially driven by differences in dispersal behavior, forest type and structure, and predation levels. Forests serve as typical winter habitats for chamois, providing essential protection from harsh conditions (Corlatti et al., 2022b). Historically, chamois have inhabited forested regions since the Pleistocene (Baumann et al., 2005), indicating the long-standing significance of forests as essential habitats for the species. Some chamois populations are primarily forest-dwelling (Corlatti et al., 2022b), and forests can also act as refuges from high temperatures (Anderwald et al., 2024) and adverse weather conditions (Ballo, 2010), even during periods when chamois utilize open habitats.

Rocky habitats (six studies) had no significant effect in the single GLM-type study considered, but they were positively selected according to two ENFA-type studies (Kati et al., 2020; Papakostas et al., 2025b) and negatively selected according to two selection ratio studies (Pépin et al., 1997; Unterthiner et al., 2012), one of which also mentioned a negative selection for escape terrain (Unterthiner et al., 2012). Rocky areas are usually associated with the species' known preference for rugged terrain and escape areas that offer protection from predators and human disturbance (Anderwald et al., 2024; Babaev et al., 2016), as well as competition mitigation with other ungulates and livestock (Chirichella et al., 2013). It is possible that in areas of high poaching activity, chamois may select rocky areas close to or within the escape terrain, while in the absence of poaching, no such limiting factor would intervene in the habitat selection process. This appears to be the case for the Maritime Alps Regional Park in Italy (Unterthiner et al., 2012), where the species avoided screes, presumably because it didn't need to hide from hunters, given the strict protection status of the Park. On the contrary, a study in the Olympus National Park in Greece, where hunting is also prohibited, but poaching still exists, the Balkan chamois selected areas near the escape terrain during the non-touristic season (winter and spring), when poaching is presumed to increase due to the absence of people and indirect control of illegal activities (Papakostas et al., 2025b). Another important reason for selecting escape terrain could be predation by wolves, as this large predator can make extensive use of chamois in his diet in some cases (Palmegiani et al., 2013).

The studies considering grassland (five studies) and bushland (four studies) as habitat selection factors showed mixed results with a positive overall score, implying that chamois rather preferred these land cover types (ENFA-type and selection ratios studies). Pattern variability likely reflects seasonal movements, as chamois shift to high-elevation grasslands from spring to autumn, where they exploit the onset of vegetation growth and associated nutritional benefits (Corlatti et al., 2022b). Variability may also arise from differences in study area locations, as bushland and grassland areas can occur at different elevation ranges across the various mountain ranges within the chamois distribution. Additional variation may stem from differences in vegetation classification, as grassland refers to both alpine and subalpine meadows, while bushlands include various types, such as scrublands or *Rhododendron* moors.

Disturbance

Disturbance variables were less frequently examined (six studies). According to our results, hunting, infrastructure, and then competition with wild ungulates and livestock were the most substantial negative factors in descending order, while hiking trails had a relatively positive influence on habitat selection (**Fig. 4.6a**). Disturbance from hunting has only been examined in a single study from Greece, where chamois hunting is prohibited nationwide, showing that chamois consistently avoided hunting areas (Kati et al., 2020). These results may reflect the inadequate hunting management practices in Greece. In contrast, in countries with well-structured management plans, hunting is not typically considered a disturbance factor in habitat selection studies. Further research is necessary to gain a clearer understanding of how hunting other species impacts chamois habitat selection.

According to two ENFA-type studies (Kati et al., 2020; Papakostas et al., 2025b), chamois consistently avoided infrastructures (roads and human settlements), highlighting the sensitivity of this species to human presence. The construction of new roads degrades habitat quality and increases anthropogenic disturbance, compelling ungulates to avoid such areas in various ecosystems worldwide (Bleich et al., 2009; Lian et al., 2012). Reducing road and other infrastructure development in remote mountainous areas and preserving wilderness would halt land artificialization and mitigate poaching pressure on chamois populations, thereby enhancing the species' conservation (Kati et al., 2023a; Kati et al., 2023b; Papaioannou, 2021). Further research is necessary to understand the long-term effects of infrastructure on chamois populations and their habitat dynamics.

Hiking trails were included as a factor in three studies examining habitat selection. They had no significant effect in the single GLM-type study (Ciach & Pęksa, 2019), whereas they showed a positive score on ENFA-type studies, involving both positive (Papakostas et al., 2025b) and negative cases (Darmon et al., 2012). Chamois typically respond to human disturbances by altering their activity patterns and avoiding areas with human presence (Kati et al., 2020; Oberosler et al., 2017; Salvatori et al., 2023), including regions frequented by hikers (Courbin et al., 2022; Pęksa & Ciach, 2018) and other recreational activities (Boldt & Ingold, 2005; Pęksa & Ciach, 2015; Schnidrig-Petrig & Ingold, 2001). However, they can become habituated to human presence in areas with high levels of hiker activity (Courbin et al., 2022; Papakostas et al., 2025b). This habituation may explain the positive effects observed in our analysis, combined with the energetic advantages of using trails for large mammals. However, it could have negative consequences in areas where chamois hunting is permitted, as they may remain tolerant of human activity even during the hunting season, potentially leading to increased mortality rates (Courbin et al., 2022). Additionally, stress levels in chamois could be elevated in areas with high tourist numbers (Zwijacz-Kozica et al., 2013).

Competition with other wild ungulates or livestock has been poorly investigated in habitat selection studies. They had no significant overall effect according to the two GLM-type studies considered, while one ENFA-type study showed a negative influence on habitat selection. The primary competitors of chamois are red deer *Cervus elaphus* (Corlatti et al., 2022b). Red deer significantly compete with chamois for habitat and resources, which adversely affects chamois survival rates (Donini et al., 2021) and elevates stress hormone levels during warmer months when red deer extend their range into chamois habitats (Formenti et al., 2018). In response, chamois may avoid areas with high red deer populations, relocating to different habitats that often have lower forage quality (Anderwald et al., 2015). However, the influence of red deer on the spatiotemporal behavior of chamois is relatively weak in forested areas (Kavčić et al., 2021b). Another ungulate species that can influence the spatial behavior of chamois is the mouflon (Chirichella et al., 2013). Livestock also represents an important stress factor, as in areas where sheep or goats are present, fecal cortisol metabolites (FCM) in chamois are elevated (Formenti et al., 2018). Chamois also tend to remain closer to escape terrain when livestock herds are nearby, particularly in the presence of guardian dogs (Chirichella et al., 2013). Given the limited research on the chamois competition with both wild and domestic ungulates, we propose further research in this field to enhance our understanding of these interactions and their impact on the habitat use behavior of the species.

Climatic

Climatic variables had no significant overall effect based on a single GLM-type study (Anderwald et al., 2024), while appeared generally neutral or produced inconsistent results based on three ENFA-type studies (Anderwald et al., 2016; Darmon et al., 2012; Papakostas et al., 2025b) (**Fig. 4.6a**). However, this pattern likely reflects the limited number of studies that have explicitly included climate-related variables rather than an absence of influence. In the context of accelerating climate change, future habitat selection research should prioritize climatic drivers. Rising temperatures and climate change are closely linked and can significantly impact various aspects of chamois ecology and behavior alongside other examined factors (Lovari et al., 2020). Increased temperatures may elevate stress levels in chamois (Anderwald et al., 2021b; Corlatti et al., 2023; Fattorini et al., 2023), lead to declines in body mass (Mason et al., 2014a), or declines in yearling survival (Chirichella et al., 2021). In response, chamois may alter their daily activity patterns by shifting peak activity to early morning or evening hours and increasing nocturnal behavior as a strategy to cope with elevated daytime temperatures (Grignolio et al., 2018; Thel et al., 2024) or move to forested areas that provide shelter from high temperatures (Anderwald et al., 2024). Another critical adaptation to rising temperatures is their tendency to disperse upslope in search of more favourable climatic conditions. This upward movement can reach approximately 200 meters, resulting in a substantial loss of their current habitat (Hoste et al., 2024). However, this prediction may be overstated; other research suggests that livestock presence has a more pronounced effect on upslope movement than temperature alone. Specifically, it predicts an average increase in the altitudinal range of chamois of approximately 15-30 meters by 2100; this figure rises to approximately 125 meters when accounting for livestock presence, leading to a projected 55% reduction in suitable habitat across the Alps (Mason et al., 2014b). To enhance the accuracy of predictions regarding the future distribution of chamois, it is essential to integrate vegetation models with climatic models. Failing to do so may result in overly pessimistic outcomes (Thuiller et al., 2018).

Methodological insights

The current synthesis is a systematic but non-comprehensive review, based on Scopus-indexed, peer-reviewed English-language publications. This approach was chosen to ensure methodological consistency, transparency, and reproducibility across studies. We acknowledge that relevant work on chamois ecology also exists in national journals, technical reports, and the broader grey literature; however, most of these sources identified during our preliminary search were descriptive in nature, often relying on outdated or incomparable methods for estimating home range or reporting habitat use, and did not contribute quantitative information suitable for habitat selection analyses. As a result, the present review should be viewed as a first, structured synthesis of the peer-reviewed evidence rather than an exhaustive overview of all available literature. Importantly, the detailed and well-structured database compiled (Supplementary Spreadsheet) provides a valuable foundation for future studies, including more comprehensive reviews that may incorporate additional grey literature articles. We also note that the results related to land cover types should be interpreted with caution, as habitat categories were defined differently across studies, making direct comparisons difficult. These methodological inconsistencies, together with variation in habitat availability across study areas, differences in sampling design, analytical methods, and seasonality, likely explain the observed heterogeneity of land cover factors.

Recommendations

This review synthesizes current knowledge on the home range and habitat selection of chamois. While research is growing on these topics, most knowledge derives from *R. r. rupicapra* in the Alps, reflecting its broad distribution and large population size. However, other subspecies remain comparatively underrepresented in the literature, including several that are of conservation concern. We recommend a broader geographic coverage in ecological chamois research, focusing on the least studied subspecies that are of conservation concern, as well as the better integration of telemetry methods and scientific networking. Land cover types and topographic variables were the most well-studied in habitat selection studies, while disturbance and climatic factors were far less studied. Future studies should incorporate these variables to understand better habitat selection under potential growing anthropogenic and environmental pressures. The compiled database of studies summarizing methods and results on chamois home range and habitat selection can serve as a valuable foundation for future ecological research, particularly by incorporating ecological modelling to enhance the reliability and comparability of findings.

Chapter 5. Seasonal and diel activity patterns of the Balkan chamois in Greece: first insights from camera trap data

Under Review in *Mammal Research*

Papakostas, K.; Papaioannou, H.; Gerogiannis, A.; Korakis, A.; Pappas, A.; Kati, V. (2026). Seasonal and diel activity patterns of the Balkan chamois in Greece: first insights from camera trap data.

Abstract

This study presents the first assessment of the activity patterns of the Balkan chamois (*Rupicapra rupicapra balcanica*) in Greece using camera traps, with a focus on potential differences between forested and open habitats. We deployed 49 camera traps across northwestern Greece (2015-2020), targeting areas with high chamois presence. Thirty-nine cameras yielded usable data (6,152 camera days). We quantified Relative Abundance Index (RAI) and analyzed seasonal and diel activity patterns based on independent photographic events. Chamois showed a high RAI (43), with daily activity ranging from 9:00 to 21:00 and a peak at 11:00. Chamois used both forested and open areas, but we found no substantial differences in their activity patterns between the two. Nocturnal activity was generally low but increased during autumn, coinciding with the rutting season. We recommend a systematic camera trap deployment in future studies to evaluate activity overlap with sympatric species and the effects of human disturbance on chamois behavior.

Keywords

Rupicapra; Forest; Nocturnal activity; Ungulates

Introduction

Researchers have traditionally studied animal behavior through direct observation and telemetry-based tracking (Brown et al., 2013). However, technological advances have made camera trapping a widely used, cost-effective, and non-invasive method for monitoring wildlife distribution, abundance, and behavior (Burton et al., 2015; Rowcliffe et al., 2014). These remotely activated cameras offer valuable data on species presence, population parameters, and activity patterns (Caravaggi et al., 2017; Tanwar et al., 2021), while also serving as an important tool for conservation efforts (Caravaggi et al., 2017). Additionally, they play a crucial role in assessing the impact of human disturbance on wildlife activity (Oberosler et al., 2017; Petridou et al., 2023; Salvatori et al., 2023).

The Balkan chamois (*Rupicapra rupicapra balcanica*), a subspecies of the Northern chamois (*R. rupicapra*), has an estimated population of 1,330–1,765 individuals across 30 populations in Greece (Papaioannou, 2021), showing an overall increasing trend (Anderwald et al., 2021a). Despite its protection under European legislation (Habitats Directive 92/43/EEC, Annexes II and IV), its current conservation status is Inadequate-Bad (U2) in Greece, though *Rupicapra rupicapra* has a favorable status in Europe (EIONET, 2019). Although primarily diurnal, chamois show considerable variation in daily activity patterns. Studies have reported unimodal peaks in early morning (Šprem et al., 2015), bimodal peaks at dawn and dusk (Darmon et al., 2014; Mason et al., 2014b), and multimodal patterns (Kavčić et al., 2021b), depending on various factors such as the habitat type and seasonality. Factors such as predator presence also shape activity patterns of ungulates (Heurich et al., 2014; Johansson et al., 2022; Ross et al., 2013). Although generally active during the day, chamois can exhibit nocturnal activity (Carnevali et al., 2016; Grignolio et al., 2018), particularly in response to high temperatures (Thel et al., 2024).

Our objectives were to i) provide a camera trap-based assessment of activity patterns of the Balkan chamois in Greece and ii) test whether chamois exhibited different activity patterns between forested and open habitats.

Materials and methods

Study area

We defined the study area using a Minimum Convex Polygon (MCP) based on the locations of the camera traps, in the Pindos mountain range (946 km^2) (**Fig. 5.1**). The site includes seven habitat types classified under the EUNIS system (Davies et al., 2004) (**Table A5.1**), and fall within five Natura 2000 sites and four designated wildlife sanctuaries (**Spreadsheet S1**). Pindos supports 19 chamois sub-populations (665-855 individuals), including the country's largest population on Mt. Timfi (c. 469 individuals) (Kati et al., 2020; Papaioannou, 2021).

Data collection

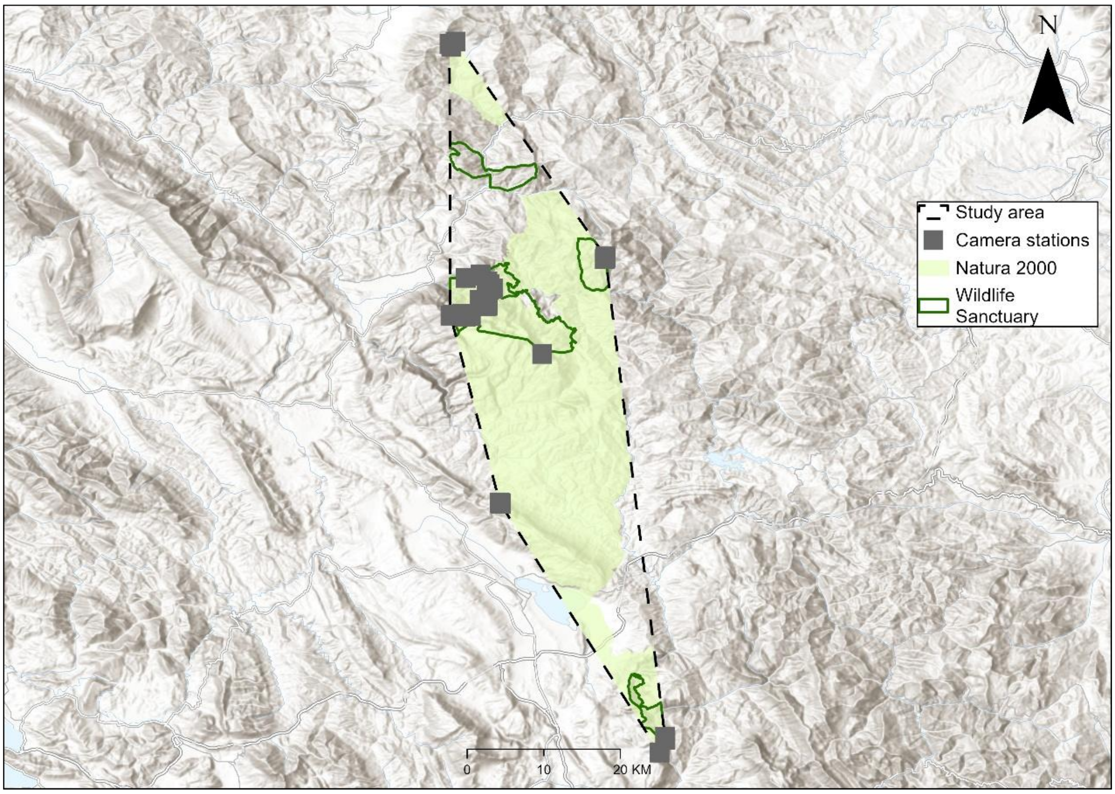

Fig. 1 Locations of camera trap stations, Natura 2000 areas, and wildlife sanctuaries in the Pindos mountain range

We deployed 49 (21 open areas; 28 forests) Bushnell® Trophy Cam HD camera traps (13/03/2015-04/09/2020), selecting localities of steep slopes, and away from roads (**Table 5.1**), to maximize the probability of recording chamois, based on expert opinion and chamois behavior in Greece (Kati et al., 2020; Papakostas et al., 2025a; Papakostas et al., 2025b). We placed cameras 50-70 cm above the ground, in photo-only mode operation, with medium sensitivity and three pictures per detection. Once installed, the cameras remained at the same locations throughout their period of operation. Field visits were limited to battery and memory card replacement. To reduce the likelihood of repeated detections of the same individuals at nearby stations within the same sampling period, camera traps in close proximity operated in different sampling periods.

Table 5.1 Description of the environmental characteristics of the camera traps localities in the study area as average values (± standard deviations), number of functional camera traps (N) in forests (G) and open areas (E) according to the EUNIS classification, total number of recording days and events of chamois records, indicating the number of all events in parenthesis

Characteristic	Value
Elevation (m)	1,637 (± 491)
Slope (º)	23 (± 9)
Distance to road (m)	1,681 (± 691)
N in forests (G)	23
N in open areas (E)	12
Recording days	6,152
Chamois events (all events)	2,645 (6,173)

Photo processing and analysis

At the end of the sampling period, we retrieved the camera traps and manually identified all images using the open-access software Wild.ID (Rovero & Zimmermann, 2016). We then exported the full database, including date, time, and species for analysis.

To reduce temporal autocorrelation, before all analysis we applied a temporal independence filter to camera-trap detections. We considered detections of chamois at the same camera station as independent events only when at least 15 minutes elapsed between consecutive records (Rovero & Zimmermann, 2016). We computed camera trap days for each camera, as the total number of 24-hour periods between deployment and retrieval, or until the last recorded image in cases where the memory card reached full capacity before retrieval. We then calculated the Relative Abundance Index (RAI) by dividing the event count by the number of sampling days and multiplying by 100. We used RAI solely as a measure of detection intensity, not as an estimate of true abundance.

Given that our sampling design focused on chamois, records of other species and human disturbance were too sparse to support an activity-overlap analysis (**Table A5.2**). To assess differences between forested and open habitats, we assigned EUNIS category G habitats as forests and categories E and F as open areas. For a balanced comparison between habitat types, we retained all cameras operating in open areas and randomly selected an equal number of the forest cameras. We performed this random selection once prior to analysis and retained the same subset of forest cameras across all seasons and analyses. To examine habitat and seasonal differences in activity, we used the package "overlap" to create kernel density estimation curves (Meredith & Ridout, 2014), and we calculated the coefficient of overlap Δ_4 between each pair (Ridout & Linkie, 2009). The coefficient Δ ranges from zero, which indicates no overlap, to one, which indicates complete overlap, and is considered high if $\Delta > 0.75$, intermediate if $0.50 < \Delta < 0.75$, and low if $\Delta < 0.50$ (Monterroso et al., 2014). We then estimated the 95% confidence intervals of the overlap coefficient using 10,000 bootstrap replicates (Rovero & Zimmermann, 2016). We conducted all analyses in R (version 4.3.0) (R Core Team, 2023).

Results and Discussion

Wildlife and human disturbance

Thirty-nine cameras (16 open areas; 23 forests) accumulated 6,152 camera days (mean per site 158±139), distributed across all months (mean per month 513±121) (**Spreadsheet S1**) (**Table A5.3**). We recorded 6,173 independent events, including 3,259 of wild mammals. Among mammal species, chamois had the most events (2,645), followed by European hare *Lepus europaeus* (175) and wild boar *Sus scrofa* (117); with the grey wolf *Canis lupus* (20) and roe deer *Capreolus capreolus* (18) rarely detected. Chamois had the highest RAI of all recorded species, with a value of 43 (**Table A5.2)**. This outcome is expected because we placed the cameras in suitable chamois habitats, characterized by steep and rugged terrain (Anderwald et al., 2024; Corlatti et al., 2022b), maximizing its detection probability, in areas of very low human disturbance and low pressure from predators or other herbivores (**Table A5.2**). These habitats likely also provide refuge from predators and reduce interspecific competition. The low detection rates of large predators may indicate that these habitats provide a degree of natural protection. However, more extensive spatial sampling is needed to confirm this.

Forest cameras (15 stations) recorded 1,317 chamois events over 5,266 camera days, while open-area cameras (15 stations) recorded 1,354 events over 1,835 days. The RAI was lower in forests (25) than in open areas (73.8). These results suggest that chamois use both habitats, but appear more frequently, or are more easily detected, in open alpine grasslands. This may reflect detectability bias, as open areas offer wider fields of view, while forested terrain limits visibility due to vegetation and slope.

Activity patterns

Chamois activity varied across months, peaking in May (551 events), June (511), and October (442), and dropping to its lowest in January (27), February (31), and December (31). Seasonally, activity was highest in summer (985 events), followed by autumn (793), spring (778), and winter (89). In forests chamois had the most events in spring (565), followed by summer (521), autumn (171), and winter (60). In open areas, autumn (621) and summer (471) had the most events, while spring (235) and winter (27) had lower numbers. Considering the full dataset and both habitat types, spring and summer showed the highest activity overlap (Δ_4=0.93, CI: 0.89–0.95), whereas summer and autumn showed the lowest overlap (Δ_4=0.74, CI: 0.71–0.78) (**Fig. A5.1**).

Chamois showed peak daily activity around 11:00, with general activity spanning from 9:00 to 21:00 across the year (**Fig. 5.2**). Both in forests and open areas, activity peaked around 11:00, while the overall activity was highly similar (Δ_4=0.88, CI: 0.85–0.90) (**Fig. 5.3**). We did not observe a clear bimodal pattern, reported in chamois (Darmon et al., 2014; Mason et al., 2014b) and other mountain ungulates (Li et al., 2020), nor a unimodal pattern (Šprem et al., 2015). Instead, activity patterns varied seasonally and were often multimodal, as observed in other populations (Brivio et al., 2016; Kavčić et al., 2021b).

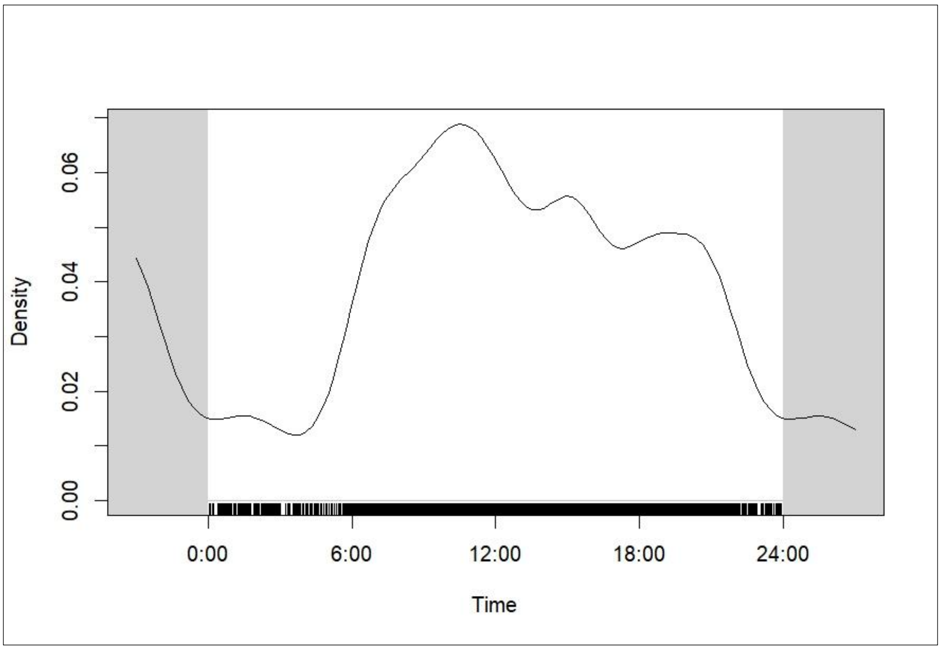

Fig. 5.2 Annual distribution of daily activity of the Balkan chamois in the Pindos mountain range

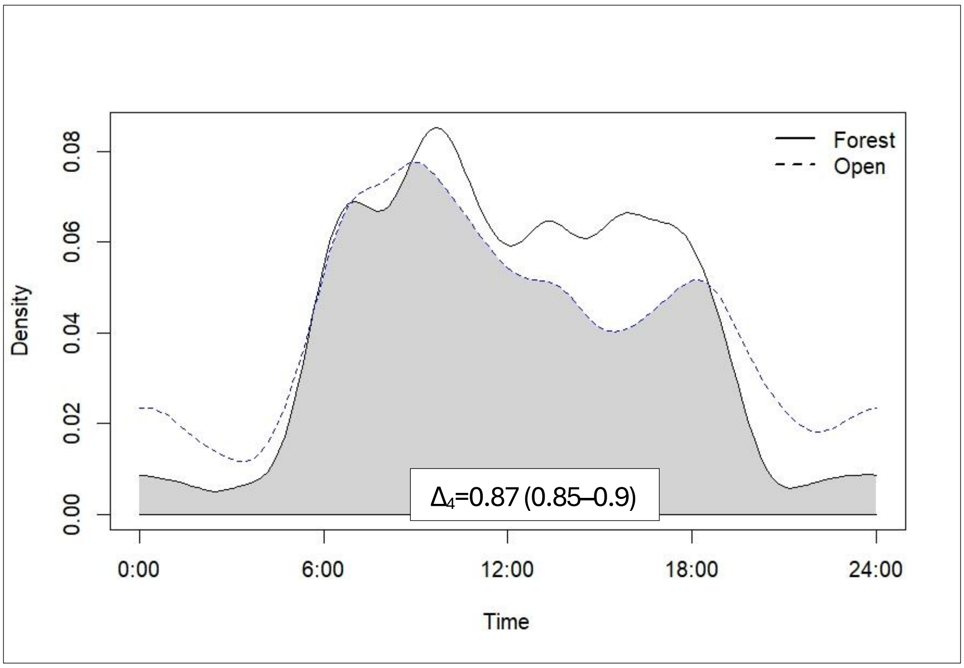

Fig. 5.3 Annual distribution of daily activity of the Balkan chamois in forested and open areas of the Pindos mountain range

In summer, chamois showed a bimodal pattern in forests and a unimodal one in open areas: forested areas had activity peaks at about 6:00 and 17:00, whereas open areas showed a single peak at about 9:00. The activity overlap between the two habitat types was high (Δ_4=0.91, CI=0.87-0.94) (**Fig. 5.4a**). In spring we also found a unimodal pattern in both areas, with a peak of activity at around 9:00, (Δ_4=0.82, CI=0.8-0.87) (**Fig. 5.4b**). A study from Croatia reported a unimodal pattern in forest-dwelling chamois, likely linked to predator avoidance (Šprem et al., 2015). This was not the case in our study sites, where predator presence was low (63 records of bear and wolf) (**Table A5.2**). In open habitats, chamois reduced their activity during the hottest hours, indicating heat avoidance (Thel et al., 2024), particularly in summer. This thermoregulatory behavior may intensify under climate change, potentially altering daily activity patterns and rut behavior (Garcia et al., 2014). Such shifts could be more pronounced in arid regions, where Balkan chamois already adjust their seasonal range in response to drought (Papaioannou et al., 2015; Papakostas et al., 2025b).

In autumn, chamois also displayed a high overlap in activity patterns between forested and open areas (Δ_4=0.92, CI=0.89-0.95). In autumn, the pattern was highly multimodal, with forested areas showing peaks at around 9:00 and 15:00, while open areas at around 9:00 (**Fig. 5.4c**). We suggest that, in autumn, the multimodal activity pattern and the substantially higher nocturnal activity compared to the rest of the year may occur due to the aligning with the rutting season. While nocturnal activity is reported year-round (Carnevali et al., 2016), it often intensifies during the rut (Grignolio et al., 2018), a pattern that our results may also reflect. Nocturnal activity of chamois can also increase in response to heat (Thel et al., 2024), though we did not observe such behavior during warmer months.

Winter activity was multimodal and remained relatively low in both habitat types, with a peak at about 19:00 in forests and about 9:00 in open areas (**Fig. 5.4d**). The limited number of winter detections prevents firm conclusions about chamois activity during this season. The observed reduction in winter activity may reflect seasonal movements to lower altitudes, as reported for chamois populations elsewhere (Corlatti et al., 2022b), although our data do not allow direct evaluation of this process. Reduced food availability and deep snow may further restrict winter movement (Brivio et al., 2016). Overall, we found no significant differences in activity patterns between forested and open areas. Similar patterns have been reported for Alpine chamois (Šprem et al., 2015).

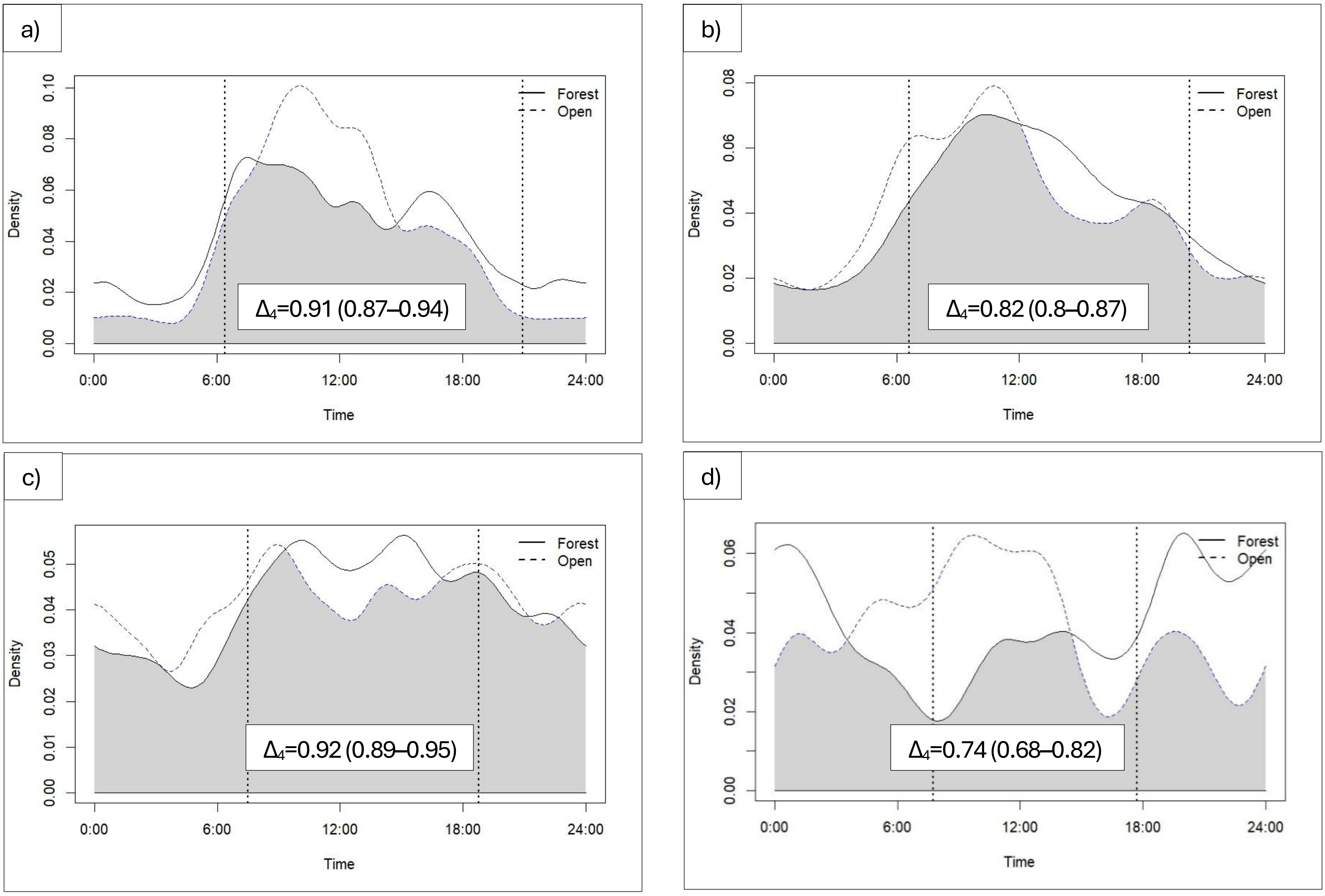

Fig. 5.4 Seasonal distribution of Balkan chamois activity in forested and open areas of the Pindos mountain range: a) summer, b) spring, c) autumn, d) winter. Vertical dashed lines represent the average sunrise and sunset times

Research perspectives

In this study, we adopted a camera-trap design aimed at maximizing the probability of detecting Balkan chamois in order to provide a first assessment of the species' diel and seasonal activity patterns in Greece. Camera placement was opportunistic and targeted areas of high chamois use, which limits spatial independence and precludes strict comparability of sampling effort across seasons and years. Consequently, the activity patterns presented here should be interpreted as descriptive patterns associated with high-use areas. Although camera placement did not avoid spatial autocorrelation, our study did not aim to estimate density or abundance, which require spatial independency of the cameras. Instead, we focused on describing diel and seasonal activity patterns, which emphasize the temporal distribution of detections. This targeted design also limited our ability to perform comparative activity analyses with other species or to assess the effects of human disturbance. Future studies should therefore deploy camera traps using systematic and spatially balanced designs across habitat types and elevation gradients, enabling robust evaluation of interspecific interactions, and anthropogenic impacts. Further research is also recommended on chamois activity patterns in drier and hotter Mediterranean mountain systems, where behavioral plasticity may become increasingly important under ongoing climate warming.

Funding

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Appendices 5

Table A5.1 Total area (km^2) of the habitat types at the two study areas, based on the EUNIS classification system (Davies et al., 2004)

Label	Habitat	Pindos (km^2)
C1	Surface standing waters	6.6
C2	Surface running waters	0.4
D5	Sedge and reedbeds, normally without free-standing water	0.7
E1	Dry grasslands	44.1
E2	Mesic grasslands	7.1
E3	Seasonally wet and wet grasslands	5.2
E4	Alpine and subalpine grasslands	25.9
F2	Arctic, alpine and subalpine scrub	37.1
F3	Temperate and mediterranean-montane scrub	0.1
F5	Maquis, arborescent matorral and thermo-Mediterranean brushes	24.1
FB	Shrub plantations	0.05
G1	Broadleaved deciduous woodland	313.5
G3	Coniferous woodland	220.5

G4	Mixed deciduous and coniferous woodland	106.3
G5	Lines of trees, small anthropogenic woodlands, recently felled woodland, early-stage woodland and coppice	62.5
H2	Screes	5.2
H3	Inland cliffs, rock pavements and outcrops	8.6
H5	Miscellaneous inland habitats with very sparse or no vegetation	12.3
I1	Arable land and market gardens	31
I2	Cultivated areas of gardens and parks	0.1
J1	Buildings of cities, towns and villages	0.8
J2	Low density buildings	4.3
J3	Extractive industrial sites	0.1
J4	Transport networks and other constructed hard-surfaced areas	1.6

Table A5.2 Relative Abundance Index (RAI) and Relative Frequency of Registrations (RFR) per event category for 6,152 camera trap days (2015-2020; 39 camera traps) in Pindos mountain range

Category	Species	Events	RAI	RFR	RFR per category
Chamois	*Rupicapra r. balcanica*	2,645	43	0.43	0.43
	Ursus arctos	43	0.7	0.007	
Chamois predators	*Canis lupus*	20	0.32	0.003	0.01
Other herbivores	*Capreolus capreolus*	18	0.29	0.003	0.003
	Canis lupus familiaris	66	1.07	0.01	
	Ovis / Capra aries / hircus	52	0.84	0.008	
Human disturbance	Humans (shepherd, hunter, hiker)	48	0.78	0.008	0.03
	Lepus europaeus	175	2.84	0.03	
	Vulpes vulpes	115	1.87	0.02	
	Sus scrofa	117	1.9	0.02	
	Martes sp.	51	0.83	0.008	
Other mammal species	*Meles meles*	49	0.8	0.008	0.08
Bird species	-	78	-	-	-

Unidentifiable objects/Blank Photos	-	2,618	-	-	-
Total	-	6,173	-	-	-

Relative Frequency of Registrations (RFR): a given species detections divided by all recorded events

Table A5.3 Camera-trap sampling effort used to describe seasonal activity patterns of the Balkan chamois in the Pindos mountain range. The table reports, for each season and month, the number of active camera-trap stations, the total number of stations active per season, and the percentage of active stations relative to the total number of deployed stations (n = 39)

Season	Month	Active camera stations per month	Active camera stations per season	% of the total stations
Winter	December	14	22	56.4
	January	19		
	February	16		
Spring	March	14	28	71.8
	April	21		
	May	24		
Summer	June	24	34	87.2
	July	18		
	August	17		
Autumn	September	16	22	56.4
	October	15		
	November	11		

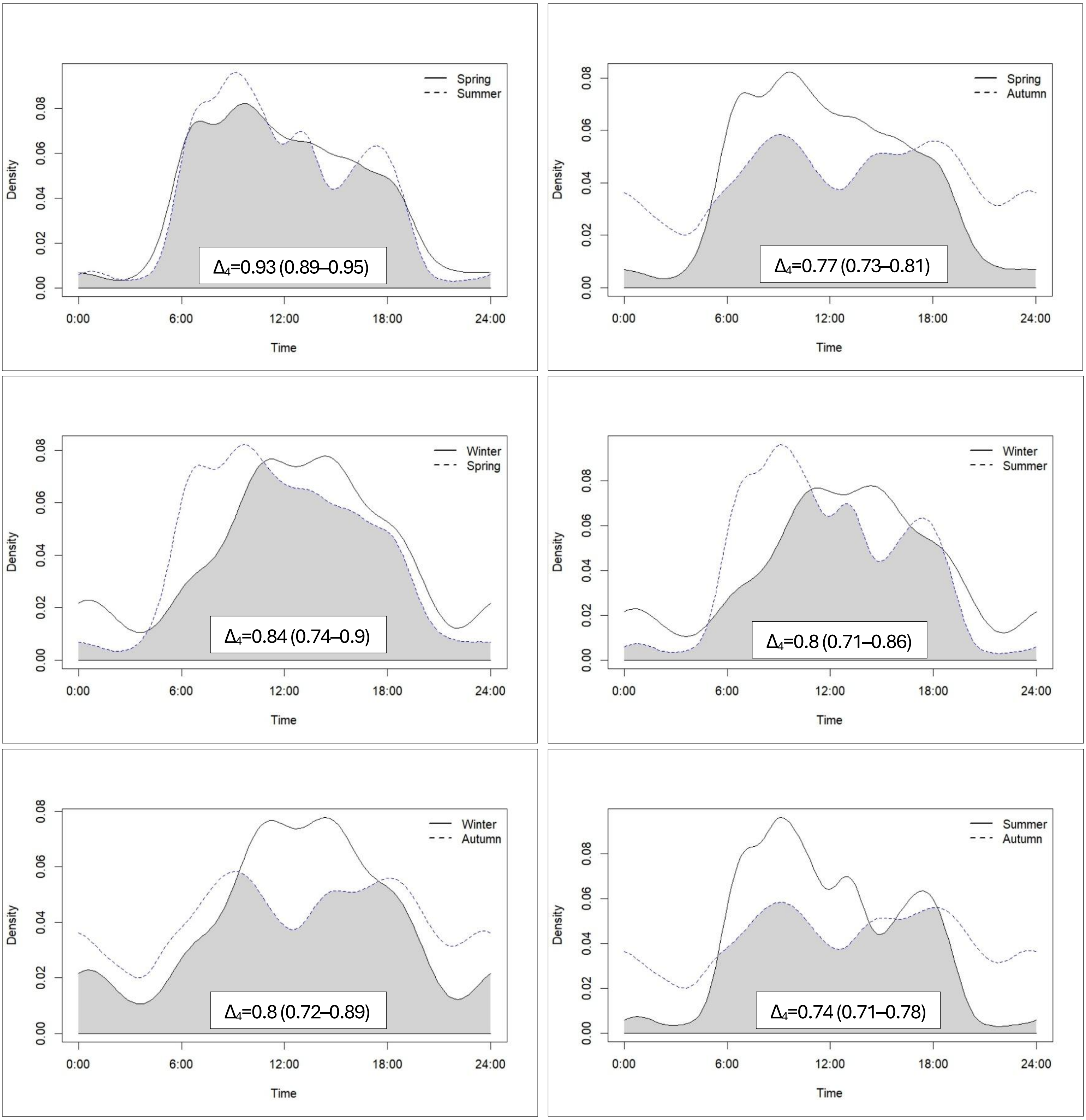

Fig. A5.1 Activity overlap of the Balkan chamois among seasons in the Pindos mountain range

General Discussion and Synthesis

Overview

This thesis aimed to improve the ecological knowledge and conservation of the Balkan chamois in Greece by combining fieldwork, spatial modelling, behavioral analysis, and a wider review of the current knowledge on the species. I examined seasonal range patterns and habitat selection in two mountains with different climatic conditions (Olympus: dry; Oiti: wet), analyzed diel and seasonal activity patterns at a regional scale, and evaluated the potential impacts of renewable energy infrastructure. I also synthesized existing research on home range and habitat selection for both Northern and Southern chamois. Together, these components offer an integrated view of the species' ecology and can better inform conservation measures.

Seasonal Population Range Patterns

Mt. Olympus and Mt. Oiti represent two mountains with different climatic and habitat conditions and provide a valuable comparison. The chamois on Mt. Olympus showed clear seasonal variation in range use, with the warm period emerging as the main stress period (Papakostas et al., 2025b). Summer and autumn had the smallest population range areas, which reflects the Mediterranean seasonal range pattern, where summer drought constitutes the major ecological constraint (**Table 6.1**). In addition, Mt. Olympus lacks permanent water sources above 1,000 m during the warm season. As a result, chamois rely on morning grass dew or on snow remnants in shaded areas to meet their water requirements. The limestone bedrock of Mt. Olympus likely explains the absence of permanent surface water. Similarly, the limestone substrate of Mt. Giona, combined with dry conditions during the warm period, leads chamois to follow the Mediterranean seasonal range pattern (**Table 6.1**) (Papaioannou et al., 2015).

In contrast, Mt. Oiti showed limited seasonal shifts, with small differences among seasons and high overlap between seasonal ranges (**Table 6.1**) (Papakostas et al., 2025a). The geological substrate, characterized by a high proportion of flysch, together with increased water and forage availability, likely explains the reduced need for seasonal movement on Mt. Oiti, where numerous mountain streams and grasslands occur.

The presence of flysch and the high annual precipitation on Mt. Timfi lead the local chamois population to follow a typical Continental seasonal range pattern (**Table 6.1**) (Kati et al., 2020), similar to that observed in other European mountain systems, where the cold period represents the main ecological constraint.

Overall, these differences highlight the strong influence of local climate and landscape structure on chamois spatial ecology and reveal the considerable plasticity of the species. Different populations can adjust their behavior to local conditions and successfully persist under contrasting environmental settings, even when the geographic distance between populations remains relatively small.

Table 6.1 Annual and seasonal population ranges (km^2) of the Balkan chamois in four Greek mountains, together with annual precipitation (mm) and the corresponding seasonal range use pattern

Mountain	Annual Precipitation	Annual Range	Spring range	Summer range	Autumn range	Winter range	Seasonal pattern
Olympus	841	103	140.3	86.2	43.2	201.2	Mediterranean
Oiti	854	50	32.9	31.5	36.9	36.6	Stable
Timfi	1,560	64.9	34.1	40.2	35.6	32.1	Continental
Giona	1,191	55	43.2	16.7	30	35	Mediterranean

Habitat Selection Across Mountains

Despite the ecological contrast between Mt. Olympus and Mt. Oiti, several consistent habitat preferences emerged. The chamois favored steep and rocky areas that provide secure escape terrain, especially during spring and winter. This preference aligns with the ecology of the species, where escape terrain availability strongly shapes space use (Corlatti et al., 2022a). Topography represents one of the most extensively studied habitat selection categories, as highlighted in Chapter 4, with 13 studies and 162 reported cases. Steep slopes, elevation, and escape terrain consistently showed positive selection by chamois, which closely aligns with the findings from Mt. Olympus and Mt. Oiti.

Human disturbance also played a major role on both mountains. The chamois on Mt. Olympus tolerated proximity to hiking trails, likely due to habituation to hikers, but avoided roads. On Mt. Oiti, the species avoided roads, livestock pens, and hunting grounds. These results align with previous findings from Mt. Timfi in Greece (Kati et al., 2020), and show that human disturbance can strongly influence habitat selection. The review presented in Chapter 4 further supported these findings. Human disturbance accounted for 42 cases across six studies, with hunting emerging as the most negatively selected factor, showing negative selection in all six cases. Infrastructure followed as the second most negatively selected factor, with 15 negative and one neutral response out of 16 cases. Land cover factors do not exert a consistent influence on chamois habitat selection, as their effects depend strongly on the study area and the season. For example, chamois on Mt. Oiti occupy mainly forested habitats throughout the year, whereas on Mt. Olympus they select forested areas primarily during winter. Land cover variables formed the most extensively studied habitat selection category in Chapter 4, with 13 studies and 203 cases, which highlights their importance for chamois habitat selection while also confirming the inconsistent selection patterns of most land cover factors. It is also important to clarify that we mainly address habitat selection rather than habitat preference, since the true preferences of the species may not be available within a given study area, or in some cases, preferred habitats may remain inaccessible due to external constraints, such as human disturbance (e.g. chamois may use forested habitats during summer instead of open grasslands because of human disturbance in the grasslands).

Activity Patterns

The activity analysis revealed moderate to high overlap among seasons, with a main peak in the morning. Chamois showed no significant difference in activity patterns between forested and open areas, which aligns with results from Croatia (Šprem et al., 2015). The species increased nocturnal activity during the rutting period, a pattern also reported in other chamois populations (Grignolio et al., 2018). Chamois reduced their activity in open areas during the hottest hours of summer, indicating heat avoidance as documented in other studies (Thel et al., 2024).

Threats and Pressures

The thesis findings confirm that human disturbance represents one of the most important pressures on the species. Poaching remains the major threat in Greece, particularly for isolated populations with limited ability to recover. Roads, livestock activity, and hunting areas act as strong negative predictors of habitat selection. Renewable energy infrastructure also poses a growing threat, since many planned projects overlap with suitable chamois habitats. Tourism and climate change add further stress, especially in mountainous regions already affected by drought and habitat degradation. However, the Balkan chamois population on Mt. Olympus appeared to benefit from the presence of hikers, likely because human presence reduced poaching risk (Papakostas et al., 2025b). Fragmented populations with weak connectivity face an increased risk of genetic isolation, which reduces the long-term viability of the species. These threats interact across spatial scales and require coordinated management across regions and administrative boundaries, as well as collaboration with neighboring countries.

Methodological Contributions

This thesis contributes several methodological advances. I developed an approach for mapping escape terrain by combining slope steepness with spatial extent, which improved the ecological interpretation of habitat models. I applied seasonal ENFA for chamois in Greece, providing a useful framework for habitat selection analysis when telemetry data are limited. I integrated renewable energy infrastructure into species distribution models, which offers guidance for spatial planning decisions. I produced the first activity pattern analysis for Balkan chamois in Greece, using camera trap data. I also synthesized the global literature on habitat selection and home range, which places the Greek findings in a broader ecological context and supports cross-regional comparisons.

Conservation Implications

The thesis findings have strong relevance for conservation planning and align with the measures proposed in the National Action Plan (Papaioannou, 2021).

Expanding hunting-ban zones to cover suitable habitat would substantially improve protection of the species, while maintaining roadless areas and limiting new road construction would reduce poaching risk and overall human disturbance. Greece follows a hunting system that differs markedly from those implemented in most other European countries, where clearly designated hunting grounds facilitate the application of structured hunting management plans and species-specific conservation measures. In Greece, hunting is permitted almost everywhere, except within hunting-ban areas such as wildlife sanctuaries, national park core zones, and residential areas. This policy prevents effective management, as it makes it impossible to accurately control harvest numbers, detect violations, or monitor population size in order to define sustainable harvest limits. As a result, the current framework creates significant challenges for both conservation authorities and hunters. The first rough estimate of the total hunting-ban area in Greece in 2019 reached 21,842.37 km^2, which corresponds to 16.54% of the country, while areas where hunting was prohibited specifically for wildlife conservation covered 9.16% of Greece (Kati et al., 2020). An update of the hunting legislation is therefore necessary, moving towards a single and clearly defined legal framework that establishes an explicit hunting system and management plan, comparable to those applied in other European countries.

Water provision in dry mountains, such as Mt. Olympus and Mt. Giona, would support chamois populations during the warm period, a management practice already applied in other countries, for example on Mt. Biokovo in Croatia (Nikica Šprem, personal communication, 2025). We recommend the establishment of artificial water holes or water troughs in arid mountain areas within the chamois distribution range, combined with regular monitoring to ensure refilling and maintenance. This measure would not only mitigate water limitation during summer but also offer an opportunity for further research on how artificial water sources influence the spatial ecology and behavior of the Balkan chamois.

Livestock management in key pastures is also important to ensure forage availability and to reduce competition and disturbance caused by sheepdogs. We recommend a comprehensive assessment of habitat carrying capacity across the chamois distribution range in order to determine sustainable livestock numbers that do not create resource limitation for chamois and other wild herbivores. Such information would facilitate the implementation of sustainable grazing plans. These plans should also account for additional pressures on chamois arising from shepherd dog disturbance and displacement, as well as the risk of disease transmission.

Spatial planning should prevent the placement of renewable energy projects within suitable chamois habitat and high-quality movement corridors. This includes discouraging large-scale renewable energy developments, other land-consuming projects, and associated road expansion, given their expected negative impacts on chamois populations. Greece has already implemented a roadless policy that provides strict, although provisional, protection to nine remote mountains of high natural value (Kati et al., 2023b; Kati et al., 2022), benefiting the chamois populations. In addition, the Greek government aims to protect 55 mountains under target 15.4 of the Sustainable Development Goals, which focuses on the conservation of mountain ecosystems (Hellenic Republic, 2022; UN, 2015). These initiatives align with the National Action Plan, which recommends the expansion of roadless areas and the modification of major construction projects through alternative solutions within the species' distribution range.

Strengthening cross-border collaboration across the Balkans remains essential for the long-term conservation of the Balkan chamois. Several Greek populations occur close to international borders, including Mt. Nemertsika, Rhodope, and Mt. Grammos, which makes cooperation necessary for effective monitoring and the prevention of poaching incidents. Coordinated cross-border responses following illegal activities would further enhance conservation effectiveness and population security.

Research Limitations

The analysis faced several limitations. The absence of telemetry data restricted the ability to describe fine-scale movement and habitat selection at the individual level. The camera trap dataset also lacked a spatially systematic sampling design, which limited the assessment of potential competition with other ungulates, predator avoidance, and human disturbance.

Future Directions

Future studies on the Balkan chamois in Greece should incorporate GPS collar data to better assess the spatial ecology of the species, while also accounting for individual and sex-specific variation. GPS collars can also provide robust information on activity patterns by allowing the identification of behavioral states, an aspect that even systematic camera trap monitoring cannot fully capture.

In addition, future research should aim to update and refine the national habitat suitability map for the species and to assess potential habitat loss and fragmentation under different climate change scenarios and renewable energy development pathways.

Final Remarks

This thesis provides a comprehensive assessment of the ecology and conservation needs of the Balkan chamois in Greece. It highlights both the resilience and the vulnerability of the species and offers practical guidance for strengthening protection at local, national, and regional scales. The work contributes to the scientific foundation needed to implement the National Action Plan and supports broader conservation efforts across the Balkans.

Authors' contribution

Chapter 2

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PhD candidate contribution: >80%

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Chapter 4

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Chapter 5

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Pappas, and Vassiliki Kati], ...; Funding acquisition: [Vassiliki Kati, Konstantinos Papakostas], ...; Resources: [Vassiliki Kati, Haritakis Papaioannou, Athanasios Gerogiannis, Athanasios Korakis], ...; Supervision: [Vassiliki Kati]

PhD candidate contribution: >70%

Publications and Congress announcements

Publications

- Papakostas, K.; Papaioannou, H.; Apollonio, M.; Kati, V. (2025). Seasonal distribution pattern and habitat selection of the Balkan chamois on Olympus mountain: Summer heat, hikers, roads. Journal for Nature Conservation, 83, 126773. https://doi.org/10.1016/j.jnc.2024.126773
- Papakostas, K.; Astaras, C.; Kati, V. (2025). Mapping Balkan chamois habitat use and assessing human disturbance and renewable energy impacts on Mount Oiti, Greece. Discover Conservation 2, 29. https://doi.org/10.1007/s44353-025-00050-2
- Papakostas, K., Chirichella, R., Apollonio, M., & Kati, V. (2026). Home Range and Habitat Selection of Chamois: A Systematic Review and Meta-Analysis. Mammal Review, 56(1), e70023. https://doi.org/10.1111/mam.70023

Congress Announcements

- Poster Presentation at the 11th Hellenic Conference of Ecology (HELECOS): Ecology and Conservation of Balkan Chamois in Greece: Insights from Seasonal Range Patterns on Mount Olympus (Patras, Greece, 4-7 October 2023).
- Oral presentation at the 9th World Conference on Mountain Ungulates: Seasonal Distribution and Habitat Selection of the Balkan Chamois (*Rupicapra rupicapra balcanica*) Under Climate Change and Habituation to Hikers (October 12-14, 2024, Dushanbe, Tajikistan-online).
- Oral Presentation at the 12th Hellenic Conference of Ecology (HELECOS): Human Disturbance and Wind Energy Development: Threats to the Balkan Chamois (*Rupicapra rupicapra balcanica*) on Mount Oiti (Athens, Greece, 1-4 October 2025).
- Oral presentation at the “Genetic adaptation of Northern chamois (*Rupicapra rupicapra* L.) ecotypes to climate change and habitat loss: A case study on the endangered subspecies of Balkan chamois (*R. r. balcanica*)” workshop: Ecology and Conservation of the Balkan chamois (*Rupicapra rupicapra balcanica*) in Greece (Mitrovac na Tari, Serbia, 03/2025)

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