

## Research Article

# Home range in genus *Capra*: from polygons to Brownian bridges of scabietic and healthy Iberian ibexes (*Capra pyrenaica*)

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## Abstract

Home range and home range overlap can be used to describe use of space and movement of wildlife. During the last years, advancements in technology have greatly improved our understanding of animal movement, especially among large herbivores. Wild ungulate abundance and distribution have increased in temperate areas. Moreover, their diseases—including sarcoptic mange in the Iberian Ibex (*Capra pyrenaica*)—have become a cause of concern for livestock, public health, and wildlife conservation. In this study, we first reviewed existing literature on the home range of species in the genus *Capra*. We then analyzed data from 52 GPS-GSM-collared Iberian ibexes, of which 33 were healthy and 19 were affected by sarcoptic mange from 3 different populations in the southeastern Iberian Peninsula to analyze: (1) differences in size and characteristics of home ranges obtained by the 3 most commonly used methodologies—minimum convex polygon, kernel density estimation, and Brownian bridges movement models (BBMMs); and (2) the impact of endemic sarcoptic mange on Iberian Ibex home range. The literature review revealed that available information on spatial behavior of *Capra* spp. was based only on 3 species, including the Iberian Ibex, estimated through a diversity of methods which made it difficult to compare results. We found positive correlations among the different home range estimation methods in the Iberian Ibex, with BBMMs proving to be the most accurate. This study is the first to use BBMMs for estimating home range in this species, and it revealed a marked seasonal behavior in spatial use, although sarcoptic mange smoothed such seasonal pattern. The seasonal overlaps obtained suggest that core areas of the Iberian Ibex change within wider home range areas, which are ecological parameters relevant to identifying key areas for species management and conservation.

**Key words:** Brownian bridge, *Capra pyrenaica*, GPS-GSM, kernel density estimation, minimum convex polygon, sarcoptic mange, spatial behavior, systematic review.

Home range is defined as the surface occupied by an individual during a time period to fulfill its physiological activities (Burt 1943). It is characterized by size, shape, and structure (Kenward 2001), and its estimation is affected by time scale, individual characteristics, and methodology. Home range overlap is used to assess the spatial proportion shared by individuals and/or among periods, providing information about social relationships, site fidelity, and migratory behavior (Fieberg and Kochanny 2005;

Winner et al. 2018). Home ranges vary among wild ungulate species and populations, both temporally and spatially (Börger et al. 2006a; Rivrud et al. 2010), depending on factors including resource availability, seasonality, human activities, predation avoidance, physiological and reproductive status, or social organization (Börger et al. 2006a; van Beest et al. 2011; Berger-Tal and Slatz 2019). Larger home ranges provide greater resource availability and reproduction probability, but also increase predation

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risk and energetic cost (Tamburello et al. 2015). Home range size is therefore related to the balance between metabolic needs and food acquisition capabilities (Harestad and Bunnell 1979). Consequently, using home range size as a proxy for space use is key for wildlife population conservation and management, with ecological and evolutionary implications (Ofstad et al. 2016).

European wild ungulate populations, including the Alpine Ibex (*Capra ibex*; Shackleton 1997) in Italy and the Iberian Ibex (*C. pyrenaica*) in Spain (Pérez et al. 2002) occupied scarce and isolated cores due to overexploitation and habitat destruction caused by human development during the first half of the 20th century (Putman et al. 2011). However, conservation efforts, habitat recovery resulting from rural abandonment, predator absence, and human reintroductions and translocations have favored the increase and spread of these species (Linnell et al. 2020). Following this general trend, Iberian Ibex populations have increased and expanded for the last several decades in their endemic range of mountain areas in Andorra, France, Portugal, and Spain (García-González et al. 2020). Nevertheless, threats to their conservation persist, particularly for isolated and/or genetically low diversity populations (Pérez et al. 2002, 2021). Currently, sarcoptic mange, caused by the burrowing mite *Sarcoptes scabiei*, is probably the biggest threat for Iberian Ibex conservation (Pérez et al. 2002). Sarcoptic mange led to a reduction of over 90% in the Iberian Ibex population from Sierras de Cazorla, Segura y las Villas Natural Park (hereafter, SCSV; Fandos 1991), but had a minor demographic effect on the population in the Sierra Nevada Natural Space (hereafter, SN), suggesting the development of resistance against this disease (Pérez et al. 2022). Nonetheless, sarcoptic mange has now become endemic in both populations (Espinosa et al. 2020; Moroni et al. 2021; Pérez et al. 2022).

Despite the importance of home range size and its conditioning factors for conservation and management, few studies have investigated home range in the Iberian Ibex (Escós and Alados 1992; Alasaad et al. 2013; Viana et al. 2018). Furthermore, in spite of significant advancements in understanding the biology, ecology, and epidemiology of sarcoptic mange in Iberian Ibex to support management, such as those applied in SN since 2000 (Granados 2002), to our knowledge, no study has addressed the potential effect of endemic sarcoptic mange on home ranges to date.

Our aims are to: (1) synthesize and appraise available scientific evidence on home range in the genus *Capra*; (2) assess the home ranges of free-ranging Iberian ibexes from 3 different populations in mountain massifs of the Southeastern Iberian Peninsula; (3) compare areas obtained using 3 different estimation methodologies, namely minimum convex polygon (MCP; Mohr 1947), kernel density estimation (KDE; Worton 1989), and Brownian bridges movement models (BBMMs; Walter et al. 2015); and (4) assess the potential effect of individual sarcoptic mange status on Iberian Ibex home range. Through literature review we collect current knowledge about *Capra* spp. home range studies and compare it with our results, identifying the more relevant contributions.

## Materials and methods

### Literature review

We conducted a literature review on the home range of species belonging to the genus *Capra* following reported guidelines for systematic reviews (Pullin and Knight 2009). We searched the ISI Web of Science and Google Scholar using a search string that combined keywords related to *Capra* spp. movement (“ungulate,”

“mountain,” and “home range size”) in titles, abstracts, and keywords of English-written articles published through 2021. This search yielded 58 potentially relevant articles reporting empirical studies (i.e. we excluded reviews, theoretical papers, book chapters, and conference papers) on the spatial movement of wild bovids, which were restricted to 18 articles on *Capra* species (Supplementary Data SD1).

For each publication, we recorded the following information: (1) general description (year of publication, journal, country); (2) general ecological factors (area, number of tracked individuals by sex); (3) methodology used to estimate home range (e.g. MCP, KDE, or BBMM); and (4) home range values (mean, median, minimum, and maximum if available).

### Study area

The study was conducted in 3 different areas within the Betic mountain range on the Southeastern Iberian Peninsula—SCSV, SN, and Orce Massif (OM; Fig. 1).

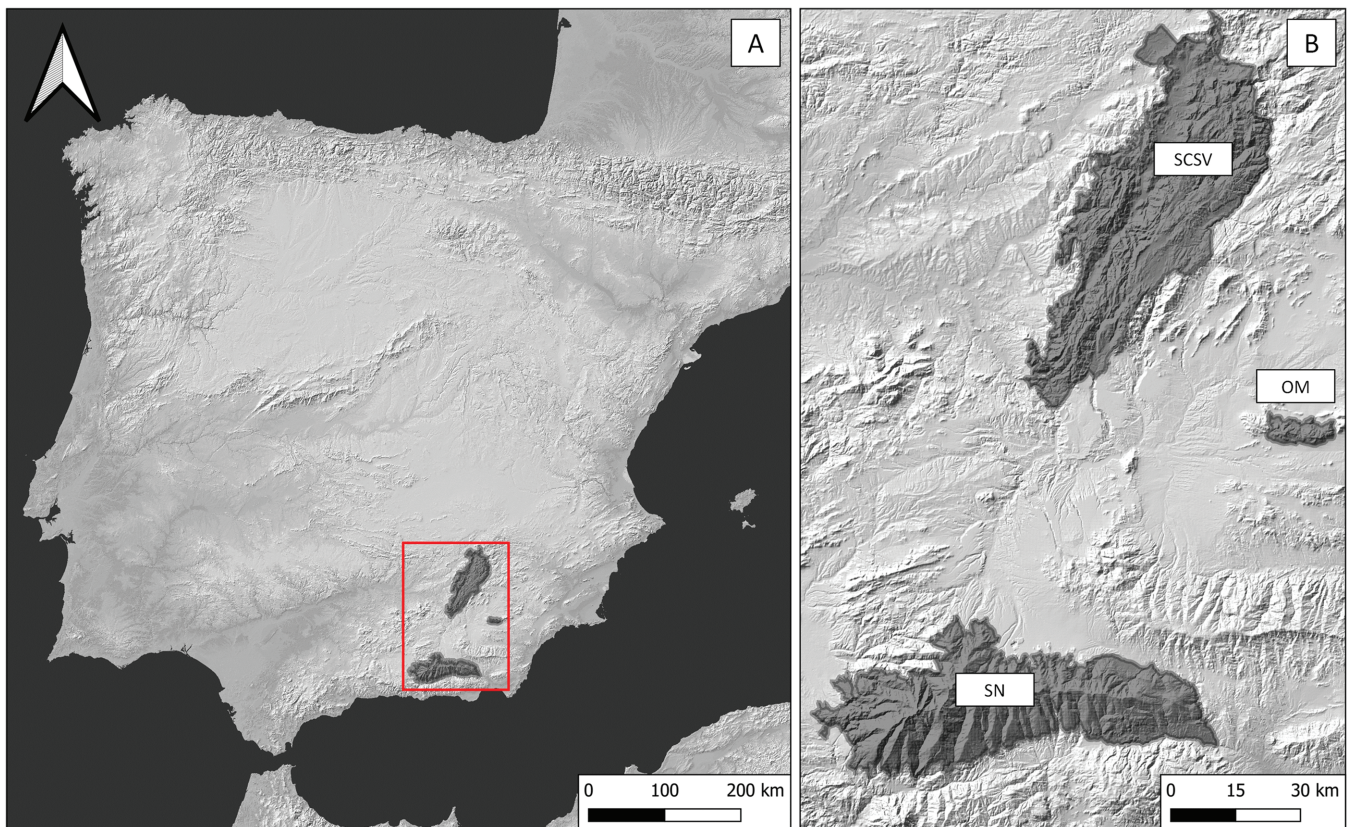
SCSV (2,143 km<sup>2</sup>) is a protected area with altitudes reaching 2,100 m a.s.l. The climate is Mediterranean, with annual rainfall ranging from 300 to 1,600 mm. The area is covered by pine (*Pinus halepensis*, *P. nigra*, *P. pinaster*, and *P. sylvestris*) and evergreen oak (*Quercus ilex* and *Q. faginea*) forests. SN is also a protected area, encompassing the core National Park (859 km<sup>2</sup>) and the peripheral Natural Park (864 km<sup>2</sup>). The climate is Mediterranean with continental traits and an annual mean precipitation over 1,000 mm. Altitude reaches 3,479 m a.s.l. (the highest summit in peninsular Spain). This wide range in altitude and climate diversity results in different biotopes including rocky peaks and valleys, deciduous oak (*Q. pyrenaica*), chestnut (*Castanea sativa*), and coniferous pine forests. OM is a 226-km<sup>2</sup> area with dry semiarid to subhumid continental Mediterranean climate, with annual mean precipitation ranging from 300 to 600 mm, and is the least productive of the 3 study areas. OM reaches 2,045 m a.s.l., and its vegetation primarily consists of evergreen oak (*Q. ilex*) and pine forests, along with shrubland and arid Mediterranean ravines.

The Iberian Ibex populations in SCSV and SN have never gone extinct in historical times (Angelone et al. 2018), whereas the Iberian Ibex population in OM originated from a recent legal population reintroduction. Sarcoptic mange is endemic in the Iberian Ibex populations in SCSV and SN (Moroni et al. 2021), while the OM Ibex population was still free from sarcoptidosis at the time of the study. Thus, by monitoring individuals from 2 established populations, where sarcoptic mange is endemic, and a recently reintroduced dispersal population, we were able to compare the effect of population status and sarcoptic mange on the movement ecology of Iberian Ibex, ensuring that at least none of the ibexes collared at OM would be affected by sarcoptic mange during the study.

### Capture and GPS collaring

Fifty-two Iberian ibexes (19 affected by sarcoptic mange and 33 apparently healthy) were marked with Global Positioning System and Global System for Mobile communication (GPS-GSM) collars and monitored from 2006 to 2019. The monitoring required at least 30 days of recorded activity. Among these ibexes, 41 were in SN (17 affected by sarcoptic mange and 24 apparently healthy), 8 were in OM (all apparently healthy), and 3 were in SCSV (2 affected by sarcoptic mange and 1 apparently healthy). Sarcoptic mange was diagnosed based on visual inspection. While this method has an 87.1% sensitivity and a 60.7% specificity for telediagnosis of sarcoptic mange on the





**Fig. 1.** (A) Study area in the Iberian Peninsula (square). (B) Shadow areas are each particular mountain systems where animals were monitored: Sierras de Cazorla, Segura y las Villas Natural Park (SCSV), Sierra Nevada Natural Space (SN), and Orce Massif (OM).

field (Valdeperes et al. 2019), for handled individuals like those in this study, this is considered absolutely reliable, being the mandatory legal test for translocating wild ungulates other than wild boar in Spain (Ministerio de Medio Ambiente, y Medio Rural y Marino 2009). The individuals that were visually diagnosed as positive for sarcoptic mange were further confirmed through mite identification in skin biopsies (Castro et al. 2018) and serological ELISA tests (Ráez-Bravo et al. 2016), as previously reported.

Throughout the monitoring period, the ibexes were tracked until they either died ( $n = 9$ ), were recaptured for collar removal ( $n = 6$ ), or the collar batteries ran out ( $n = 34$ ). Three collars were still active at the end of the monitoring period. The Iberian ibexes collared and monitored in SN and SCSV were captured and released in the same locations in these established populations, whereas the sarcoptic mange-free Iberian ibexes reintroduced in OM for population reinforcement originated from an Iberian Ibex reservoir enclosure located in SN (Granados et al. 2001; Espinosa et al. 2017).

During the capturing process, all Iberian ibexes were chemically immobilized by using a mixture of xylazine (3 mg/kg) and ketamine (3 mg/kg). Atipamezole (1 mg/10 mg xylazine) was used to revert the sedative effect of xylazine at least 1 h after dart injection in order to minimize the remaining ketamine dissociative effect (Casas-Díaz et al. 2011). Each ibex was inspected for sarcoptic mange lesions, weighted and measured, and blood, feces, cartilage and skin samples were collected according to the Iberian Ibex management plan in SN (Granados 2002). Finally, they were equipped with GPS-GSM collars Vertex Lite GSM (Vectronic Aerospace GmbH, Germany) or Microsensory System

(Microsensory SL, Spain) programmed to register positions every 1 to 4 h.

### Home ranges and overlap

We estimated Iberian Ibex home range using 3 different methods: MCP, KDE, and BBMM. MCP is defined as the smallest convex area containing all locations (Mohr 1947). KDE assigns a probability density to each location, creating isopleths of probability, such as KDE50 and KDE95, indicating 50% and 95% of probability to find the animal in that area, respectively (Worton 1989). BBMM takes into account the time between successive locations, resulting in isopleths of probability as well (Walter et al. 2015). The isopleths of 50% represent the main areas used by animals, associated with important resources named 'core areas'; whereas isopleths of 95% represent wider 'home range areas' where animals perform their physiological activities (Harris et al. 1990).

For each individual and season, we used MCP, KDE50, KDE95, BBMM50, and BBMM95 to estimate home ranges. Additionally, for individual annual areas, we estimated KDE50 and KDE95. We defined seasons as winter (January, February, and March), spring (April, May, and June), summer (July, August, and September), and fall (October, November, and December).

We also estimated seasonal and yearly overlap among home ranges for KDE50 and KDE95 for each tracked Iberian Ibex as the Bhattacharyya coefficient, ranging from 0 (no overlap) to 1 (complete overlap; Winner et al. 2018). We focused just on KDE overlaps because it is the most common method applied to estimate home range and to limit analysis and data presentation. The home ranges and overlaps were estimated with 'adehabitatHR' package (Calenge 2006) using R software ([www.r-project.org/R](http://www.r-project.org/R)).

**Table 1.** Summary of the statistical generalized linear mixed models developed in this study.

Objective	Response variable	Fix factors	Random factors	Error distribution	Link function
Detecting differences in home range and core areas depending on methodology (MCD, KDE, BBMM)	Home range Core areas	Methodology	Individual Season	Gamma	Log
Testing effects of sex, population (SN, SCSV, OM), season, and their interactions, and sarcoptic mange status (affected, unaffected) on seasonal KDE estimation of home range and core areas	Seasonal home range Seasonal core areas	Sex Population Season Sarcoptic mange status	Individual	Gamma	Log
Testing effects of sex, population (SN, SCSV, OM), and sarcoptic mange status on annual KDE estimation of home range and core areas	Annual home range Annual core areas	Sex Population	Individual Year	Gamma	Log
Testing the effects of sex, season, and sarcoptic mange status on home range seasonal overlap	Seasonal overlap	Sex Season Sarcoptic mange status	Individual Population	Binomial	Logit

## Statistical analysis

We calculated the measure of central tendencies of home ranges and overlaps as the mean values  $\pm$  standard deviation (SD). We applied this parameter because it is the most common estimate displayed in studies about the spatial behavior of *Capra* spp., which allows to compare data among our estimations and other publications (see [Supplementary Data SD1](#)).

We developed 4 different generalized linear mixed models (GLMMs) to analyze the effect of methodology, population, season, sex, and sarcoptic mange status on the spatial movement data of the GPS-GSM-collared ibexes (i.e. home ranges and overlaps; [Table 1](#)).

The first GLMM was fitted to test whether our seasonal Iberian Ibex core areas and home range estimations differed among the methodologies used (i.e. MCP, KDE, and BBMMs). Methodology was the fixed factor, whereas we included individual (i.e. collar ID) and season as random factors to avoid bias due to intraindividual behavior ([Börger et al. 2006b](#)). We used Gamma error distribution (since our response variable data were continuous with nonnegative values), and log as link function.

We fitted GLMMs to test if the KDE estimations of seasonal home range (KDE95) and core areas (KDE50) were affected by sex, population (i.e. SN, SCSV, and OM), season (including interactions among sex and season, sex and population, and season and population), and sarcoptic mange status (affected or healthy), including them as fixed factors. Again, we included individual identification (id) as a random factor, Gamma error distribution, and log as link function.

Similarly, we fitted GLMMs to test whether the KDE estimations of annual home range (KDE95) and core areas (KDE50) as response variables were affected by sex, population (including interaction among sex and population), and sarcoptic mange, including them as fixed factors. Likewise, these GLMMs included collar id and year as random factor, with Gamma error distribution, and log as link function.

Finally, to test if seasonal home range overlaps for each individual, as a response variable, were affected by the fixed factors sex, season, and sarcoptic mange, we fitted a GLMM for each KDE (i.e. KDE50 and KDE95), including collar id and population as random factors. For this analysis, we applied binomial error distribution and logit as link function.

A post hoc contrast test (Tukey) was applied for the statistically significant ( $P < 0.05$ ) variables detected through the GLMM. The 'MuMIn' ([Barton and Barton 2021](#)), 'nlme' ([Pinheiro and](#)

**Table 2.** Number of publications by species and countries. Studies: number of publications where the species spatial home range is analyzed.

Species	Country	Studies
Alpine Ibex (15)	France	4
	France-Italy	1
	Italy	9
	Switzerland	1
Iberian Ibex (2)	Spain	2
Siberian Ibex (1)	Mongolia	1

[Bates 2022](#)), and 'lme4' ([Bates et al. 2015](#)) packages were used for the GLMM modeling; while the 'Multcomp' package ([Hothorn et al. 2016](#)) was used for the post hoc contrast test. All statistical analyses were performed using R software ([www.r-project.org/R](http://www.r-project.org/R)).

## Results

### Literature review

We compiled data on home range of *Capra* spp. from 18 publications encompassing 3 species: Iberian Ibex ( $n = 2$ ), Siberian Ibex (*C. sibirica*;  $n = 1$ ), and Alpine Ibex ( $n = 15$ ; [Table 2](#); [Supplementary Data SD1](#)). The majority of these studies were conducted in Europe (Italy, France, Switzerland, and Spain; 94.4% of publications), followed by Mongolia in Asia (5.6%; [Table 2](#)). In particular, the 2 studies on Iberian Ibex home range were carried out in SN and SCSV.

Home ranges of species belonging to the genus *Capra* were mostly assessed through KDE (88.9% of reviewed publications) and MCP (77.8%), with some studies reporting multiple methods, leading to a cumulative percentage exceeding 100%. Newer home range estimation methods, such as BBMM (first described in mountain bovids in 2015), have been less frequently applied to calculate home ranges in *C. ibex* (11.1%). When more than 1 methodology was used to determine home range, MCP estimated higher values than KDE, while BBMM provided the lowest values. Among KDE methodologies, KDE95 logically tended to be higher than KDE50 ([Supplementary Data SD1](#)).



**Table 3.** Generalized linear mixed model results fitted for the different home range estimation methodologies for the Iberian Ibex (*Capra pyrenaica*) included in this study.

	Estimate	SE	t	P
Intercept	-0.23	0.004	-59.67	<0.001
BB90	1.59	0.004	422.33	<0.001
BB95	1.97	0.004	524.22	<0.001
KE50	0.58	0.004	155.84	<0.001
KE90	1.94	0.004	515.98	<0.001
KE95	2.23	0.004	591.75	<0.001
MCP	2.78	0.004	737	<0.001

In the species where specific home range sizes were described separately for males and females, home ranges were larger for males than females (Supplementary Data SD1). Variability in mean home range sizes was positively correlated with the number of home ranges reported (Supplementary Data SD1), i.e. the more home range sizes that were described for a species, the higher variability.

### Iberian Ibex monitoring

Eighty-one annual home ranges (21 from ibexes affected by sarcoptic mange and 60 from healthy ibexes) and 303 seasonal home ranges (78 from ibexes affected by sarcoptic mange and 225 from healthy ibexes) were calculated (Supplementary Data SD2).

The number of locations per individual ranged from 121 to 58,697 (mean  $4,582 \pm 8,283$  locations). The number of days with signal per collar varied from 131 to 2,901 (mean  $459 \pm 493$  days). The largest annual home range (KDE95) calculated was  $112.2 \text{ km}^2$  (observed in a male in OM) and the smallest  $0.2 \text{ km}^2$  (in a female in OM). Seasonal home ranges (KDE95) varied from  $196.7 \text{ km}^2$  (a male in OM during spring) to  $0.01 \text{ km}^2$  (a male from SN during summer).

According to the GLMM and the post hoc contrast test, home ranges estimated by all 3 methodologies differed significantly (Table 3; Supplementary Data SD2). MCP estimated the largest home ranges ( $15.6 \pm 28.7 \text{ km}^2$ ), followed by KDE (KDE50:  $2.0 \pm 4.1 \text{ km}^2$ ; KDE95:  $10.4 \pm 21.1 \text{ km}^2$ ), while BBMM estimated the smallest home range sizes (BBMM50:  $0.9 \pm 1.0 \text{ km}^2$ ; BBMM95:  $6.4 \pm 7.1 \text{ km}^2$ ).

### Seasonal and annual core areas and home ranges

The mean seasonal core area size was  $3.1 \pm 5.4 \text{ km}^2$  for males and  $0.9 \pm 1.1 \text{ km}^2$  for females, whereas the mean seasonal home range was  $15.5 \pm 28.1 \text{ km}^2$  for males and  $5.2 \pm 5.9 \text{ km}^2$  for females. The mean annual core area was  $3.8 \pm 3.8 \text{ km}^2$  for males and  $1.1 \pm 1.3 \text{ km}^2$  for females, while the mean annual home range was  $22.6 \pm 25.8 \text{ km}^2$  for males and  $6.1 \pm 5.3 \text{ km}^2$  for females (Supplementary Data SD2). In general, males had larger core areas and home range sizes than females, particularly during spring and fall (Fig. 2).

The GLMMs explaining KDE50 and KDE95 seasonal variation and the post hoc contrast tests (Table 4; Supplementary Data SD2) showed that males had significantly higher values than females in both cases ( $P < 0.001$ ), and for spring and fall seasons

( $P < 0.05$ ). Seasonal home ranges were smaller in winter ( $3.7 \pm 8.6 \text{ km}^2$ ) and summer ( $3.5 \pm 4.8 \text{ km}^2$ ) than in fall ( $7.9 \pm 12.5 \text{ km}^2$ ) and spring ( $9.3 \pm 24.7 \text{ km}^2$ ). Sarcoptic mange had no significant effect on seasonal KDE50 ( $P = 0.28$ ) nor KDE95 ( $P = 0.19$ ). Regarding populations, seasonal KDE95 in OM was significantly higher than in SCSV ( $P = 0.04$ ), whereas it did not show significant differences with SN.

The GLMM explaining annual KDE50 identified significantly higher values for males ( $P < 0.001$ ). Populations also showed significant differences among them ( $P < 0.001$ ), with OM having the highest values of annual KDE50, followed by SN, and SCSV with the lowest values. Sarcoptic mange reduced significantly estimated core areas ( $P < 0.001$ ). The GLMM fitting annual KDE95 detected significantly greater values for male than female home ranges ( $P < 0.001$ ; Table 5; Fig. 3; Supplementary Data SD2).

### Seasonal overlap

Mean seasonal overlap was  $2.9 \pm 9.3\%$  for KDE50, and  $10.8 \pm 18.1\%$  for KDE95. These values varied among the different study populations (Fig. 4), with the lowest overlap values observed in OM (KDE50 overlap:  $0.6 \pm 3.8\%$ ; KDE95 overlap:  $4.3 \pm 8.5\%$ ), followed by SN (KDE50 overlap:  $6.4 \pm 13.0\%$ ; KDE95 overlap:  $21.8 \pm 23.4\%$ ), and the highest overlap values in SCSV (KDE50 overlap:  $12.6 \pm 19.5\%$ ; KDE95 overlap:  $30.3 \pm 27.3\%$ ). The GLMM explaining KDE50 and KDE95 overlap showed higher overlaps in females than males in both cases ( $P < 0.001$ ; Table 6). Reduction of home range overlap (KDE95 overlap) related to sarcoptic mange approached significance ( $P = 0.06$ ).

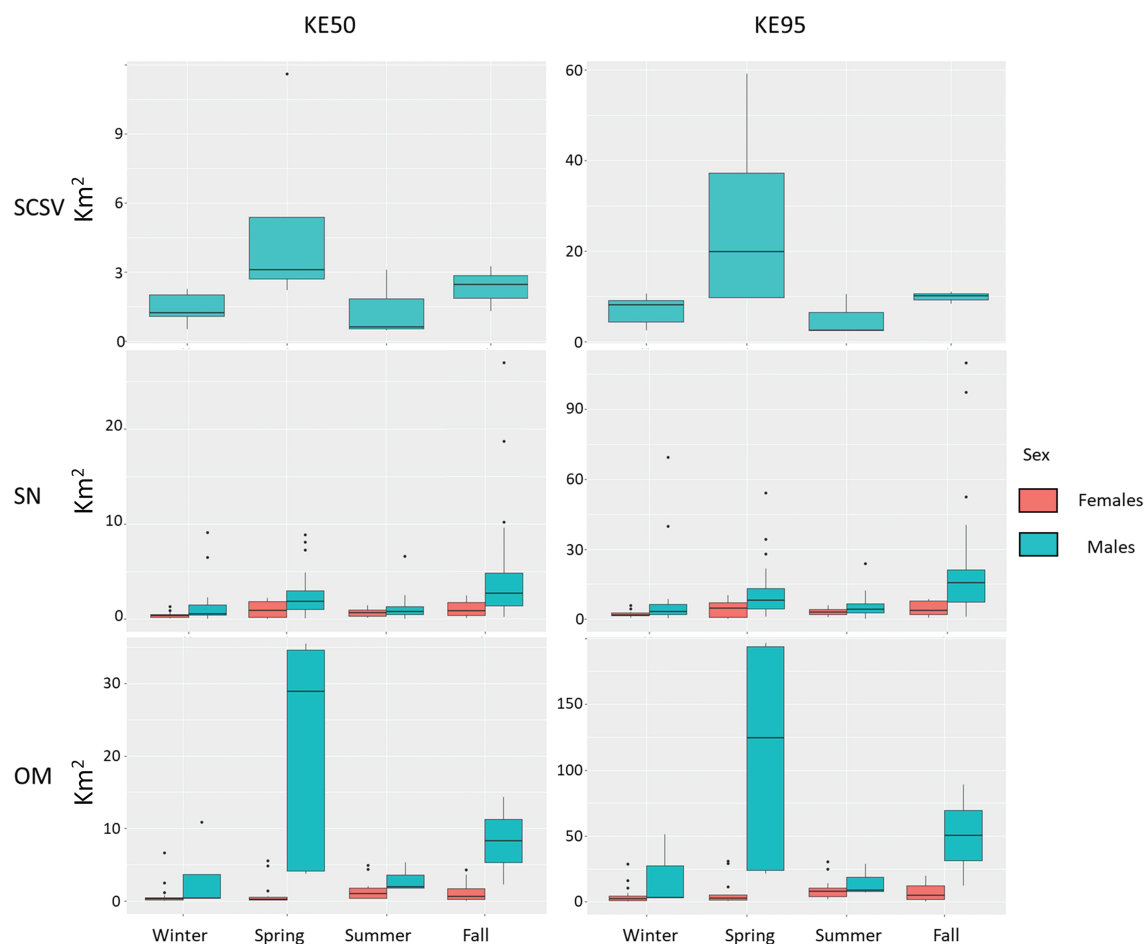
## Discussion

### Literature review

The 3 *Capra* species for which home range sizes have been reported represent 33.3% of the total 9 extant *Capra* species (Wilson and Mittermeier 2011). These studies were mostly biased toward Global North countries, as has been previously reported for wild ungulate research (Supplementary Data SD1; Pascual-Rico et al. 2021). Monitoring data from management programs not aimed at research are often not reported through scientific indexed publications but available just as “gray literature” (e.g. unpublished reports, communications in scientific meetings, articles published in languages other than English or in nonindexed journals; Fisher and Lindenmayer 2000), which could explain the scarcity of home ranges scientifically reported for *Capra* species that could be identified in the current review.

Since the interval of annual home range sizes increased with number of studies and home ranges described (Supplementary Data SD1), adding knowledge to existing information on home range sizes in Iberian Ibex is pertinent and relevant. Moreover, in contrast to previous studies that estimated home range size using MCP in SCSV (Escós and Alados 1992) and KDE50 and KDE90 in SN (Viana et al. 2018), we used BBMM for the first time to study home range in Iberian Ibex. This allowed us to compare different methodologies for home range estimation in this species. While MCP and KDE tend to overestimate home ranges (Walter et al. 2015), BBMM discriminates among individual variation (Marchand 2015) and is therefore considered more reliable.

The reviewed studies on spatial behavior in *Capra* species used different temporal scales and methodologies, which hampered comparison among species and populations. The lack of a common and standardized methodology to assess home range and core area sizes in wild species can compromise the ability to



**Fig. 2.** Seasonal core areas (KDE50) and home ranges (KDE95) of Iberian ibex populations from Sierras de Cazorla, Segura y las Villas Natural Park (SCSV), Sierra Nevada Natural Space (SN), and Orce Massif (OM) by sex and by season.

obtain common transversal conclusions regarding species management across species and populations (Laver and Kelly 2008). To avoid such drawback, monitoring and home range studies should be designed considering both the objectives pursued at a local population scale and the global scientific context. This approach would allow for transferring, sharing, and comparing results among different species and populations (Gula and Theuerkauf 2013).

### Iberian Ibex monitoring

Our results contribute to knowledge on home range sizes in Iberian Ibex, significantly increasing the previously reported interval for the species (Escós and Alados 1992; Viana et al. 2018) and using BBMMs for the first time in Iberian Ibex. We also identified larger home range sizes in male Iberian ibexes compared to females, agreeing with previous results in this species (Escós and Alados 1992; Viana et al. 2018) and in other *Capra* species (Supplementary Data SD1).

As aforementioned, when expanding the number of home ranges described for a species, the interval of home range sizes reported increases. Thus, our study widens the narrow home range intervals previously provided for the same Iberian Ibex populations (Escós and Alados 1992; Viana et al. 2018). Home range size variability may be related to habitat quality and heterogeneity (Kie et al. 2002; Oehler et al. 2003), as well as other plastic characteristics such as total energy requirement and intake,

which can adjust to environmental conditions (Brivio et al. 2014). Therefore, the heterogeneity of habitats inhabited by the studied populations and the variability of their status (established vs. dispersal/founders) could explain the wide breadth of home range sizes detected in this study compared to previously reported intervals, altogether contributing to increasing the knowledge of home range sizes and habitat requirements for this species. Such knowledge provides a completely new conceptual framework regarding environmental requirements of Iberian Ibex, with implications for the management and conservation of this species (Ofstad et al. 2016).

The different seasonal home ranges estimated by each methodology (i.e. MCP =  $15.6 \pm 28.7$  km<sup>2</sup>; KDE50 =  $2.0 \pm 4.1$  km<sup>2</sup>; KDE95 =  $10.4 \pm 21.1$  km<sup>2</sup>; BBMM50 =  $0.9 \pm 1.0$  km<sup>2</sup>; BBMM95 =  $6.4 \pm 7.1$  km<sup>2</sup>) agreed with previously reported overestimation of home range size by MCP and KDE when compared to BBMM (Walter et al. 2015). These results are also in line with findings from the literature review on *Capra* species (Supplementary Data SD1). As BBMM appear to be among the most reliable methodologies for home range estimation (Walter et al. 2015), obtaining the first home range estimations for Iberian Ibex populations using this methodology represents a significant advance in knowledge.

### Seasonality and sex-related differences

The smaller home ranges in winter and larger home ranges in spring and fall in Iberian Ibex populations could be attributed to energy-saving strategies and variation in resource availability



**Table 4.** Generalized linear mixed model fitted for seasonal core areas (KDE50) and home ranges (KDE95) for the Iberian Ibex (*Capra pyrenaica*) populations included in this study: Sierra Nevada Natural Space (SN), Sierras de Cazorla, Segura y las Villas Natural Park (SCSV), and Orce Massif (OM).

	Value	SE	t	P
KDE50 seasonal				
Intercept	-1.185	0.848	-1.397	0.16
Sex (males)	2.134	0.581	3.672	<0.001
Spring	0.331	0.780	0.425	0.67
Summer	0.004	0.846	0.004	0.99
Winter	-0.398	0.759	-0.524	0.60
SN	1.201	0.838	1.433	0.15
OM	1.327	0.812	1.636	0.10
Sarcoptic mange	0.239	0.219	1.090	0.28
Males:spring	0.141	0.351	0.402	0.69
Males:summer	-0.910	0.356	-2.555	0.01
Males:winter	-0.232	0.372	-0.625	0.53
Males:SN	-0.911	0.566	-1.611	0.11
Spring:SN	-0.802	0.733	-1.094	0.27
Summer:SN	-0.523	0.799	-0.655	0.51
Winter:SN	-0.589	0.706	-0.834	0.40
Spring:OM	-0.409	0.807	-0.507	0.61
Summer:OM	0.235	0.876	0.269	0.79
Winter:OM	-0.412	0.783	-0.526	0.60
KDE95 seasonal				
Intercept	0.305	0.792	0.384	0.70
Sex (males)	2.047	0.536	3.823	<0.001
Spring	0.890	0.748	1.189	0.23
Summer	0.079	0.802	0.099	0.92
Winter	-0.063	0.717	-0.088	0.93
SN	1.129	0.781	1.446	0.15
OM	1.586	0.761	2.084	0.04
Sarcoptic mange	0.261	0.201	1.300	0.19
Males:spring	-0.102	0.333	-0.305	0.76
Males:summer	-1.013	0.341	-2.975	<0.01
Males:winter	-0.400	0.355	-1.127	0.26
Males:SN	-0.621	0.518	-1.198	0.23
Spring:SN	-1.246	0.704	-1.769	0.08
Summer:SN	-0.492	0.756	-0.651	0.52
Winter:SN	-0.745	0.667	-1.117	0.26
Spring:OM	-0.747	0.772	-0.967	0.33
Summer:OM	0.256	0.830	0.308	0.76
Winter:OM	-0.502	0.739	-0.679	0.50

under different climate conditions. During winter, stress caused by lower resource availability and extreme climate conditions may lead to energy-saving behaviors, resulting in smaller home ranges (Willisch et al. 2013; Papaioannou et al. 2015). In contrast, during summer the abundance of high-quality habitats, such as pasture resources, may fulfill the energy requirements of the Ibex with shorter movements, leading to smaller home range sizes (Krausman et al. 1989; Oehler et al. 2003).

**Table 5.** Generalized linear mixed model fitted for annual core areas (KDE50) and home ranges (KDE95) for the Iberian Ibex (*Capra pyrenaica*) populations included in this study: Sierra Nevada Natural Space (SN), Sierras de Cazorla, Segura y las Villas Natural Park (SCSV), and Orce Massif (OM).

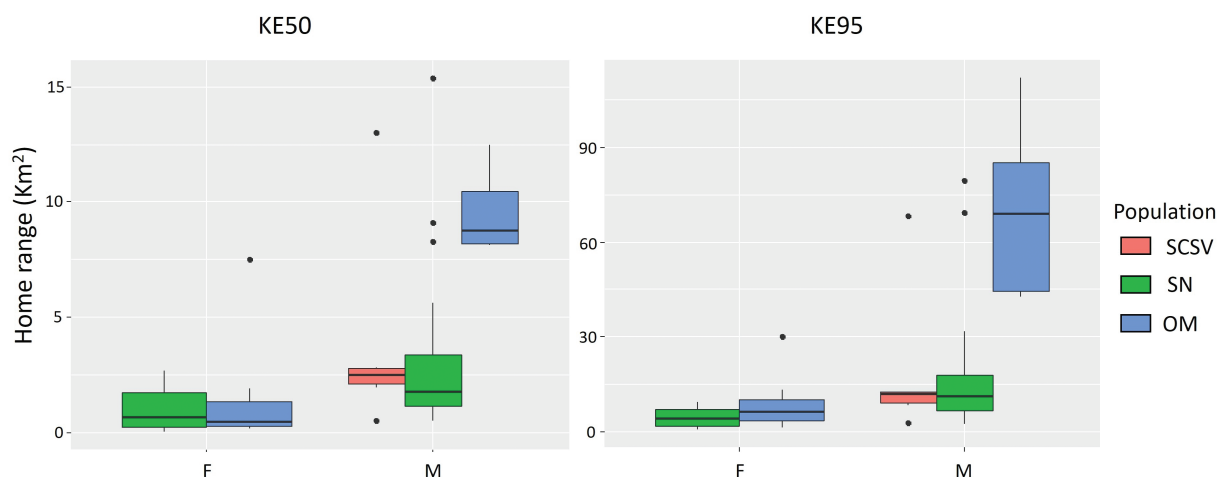
	Estimate	SE	t	P
KDE50 annual				
Intercept	-0.465	0.002	-220.50	<0.001
Sex (males)	2.022	0.002	959.50	<0.001
SN	0.387	0.002	183.50	<0.001
OM	0.404	0.002	191.70	<0.001
Sarcoptic mange	-0.446	0.002	-211.50	<0.001
Males:SN	-0.877	0.002	-416.20	<0.001
KDE95 annual				
Intercept	0.876	0.703	1.247	0.21
Sex (males)	2.072	0.506	4.092	<0.001
SN	0.631	0.718	0.879	0.38
OM	1.195	0.647	1.848	0.06
Sarcoptic mange	-0.269	0.279	-0.964	0.34
Males:SN	-0.845	0.574	-1.474	0.14

Altitudinal migration of Iberian ibexes to mountain meadows in spring, followed by descending to lower altitudes and higher slope refuge areas in fall, has been previously reported in the Iberian Ibex SN population (Granados et al. 2001; Viana et al. 2018). This behavior explains their wider home range sizes in spring and fall than in winter and summer. In mountain habitats and northern latitudes, the spatiotemporal distribution of nutrient-rich forage (Albon and Langvatn 1992) and reduction of habitat suitability due to snow (Grignolio et al. 2004) induce altitudinal migrations for food resources and protection from adverse climate conditions (Hsiung et al. 2018).

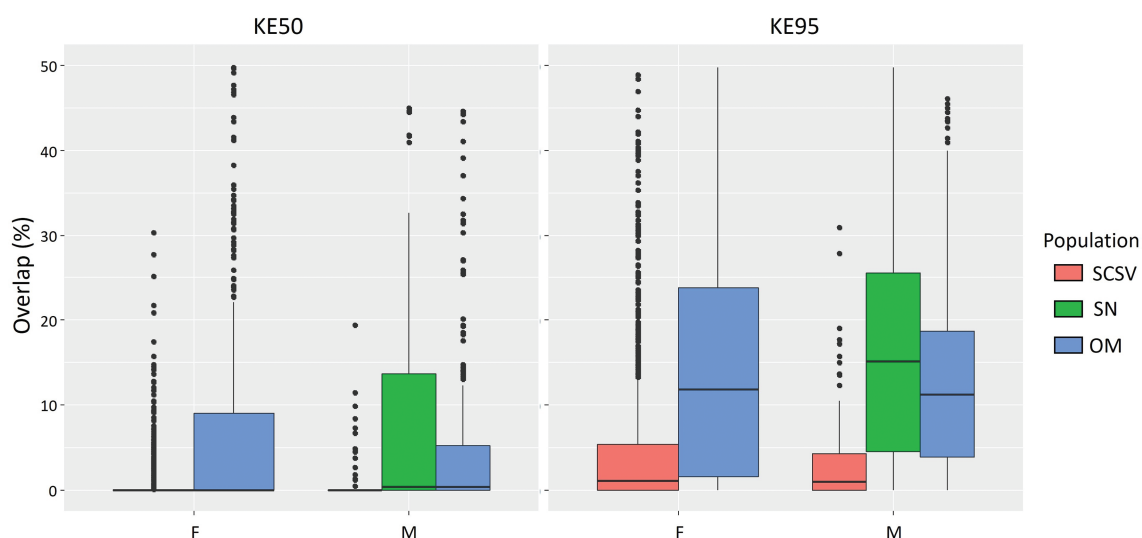
The significant difference in seasonal home ranges between male ( $15.5 \pm 28.1 \text{ km}^2$ ) and female ( $5.2 \pm 5.9 \text{ km}^2$ ) Iberian ibexes, particularly in spring and fall, agrees with previous reports in this species (Escós and Alados 1992; Viana et al. 2018) and in the closely related Alpine Ibex (Marchand et al. 2017). The greater difference between sexes in fall is probably linked to mating behavior of the Iberian Ibex. During mating season, males may significantly increase their home ranges to find receptive females and compete with other males for mating opportunities (Shakeri et al. 2021). Additionally, increase in both male and female home ranges in spring may be related to the seasonal altitudinal migration to mountain meadows (Viana et al. 2018). Furthermore, reduction in female home range size after giving birth is likely due to the restricted mobility of their newborn kids (Garfelt-Paulsen et al. 2021).

### Population differences

The larger annual core area and home range sizes observed in the reintroduced OM population of Iberian Ibex could be attributed to its recent settlement in the new area. When populations are newly introduced to a habitat, individuals may exhibit exploratory behavior as they search for the most suitable areas for survival and resource utilization. This exploratory behavior could lead to larger home ranges, as seen in other wild ungulate species (Scillitani et al. 2012a). Additionally, lower resource availability in OM compared to SN or SCSV may also contribute to larger home



**Fig. 3.** Annual core areas (KDE50) and home ranges (KDE95) of Iberian Ibex by sex and populations from Sierras de Cazorla, Segura y las Villas Natural Park (SCSV), Sierra Nevada Natural Space (SN), and Orce Massif (OM).



**Fig. 4.** Boxplot of the seasonal core areas (KDE50) and home ranges (KDE95) overlaps of Iberian Ibex by sex and populations. SCSV: Sierras de Cazorla, Segura y las Villas Natural Park; SN: Sierra Nevada Natural Space; OM: Orce Massif.

ranges. In habitats with limited resources, animals may need to cover larger areas to meet their needs, leading to increased home range sizes (Krausman et al. 1989; Oehler et al. 2003).

The differences between SN and SCSV populations could be due to altitudinal migration of ibexes in the former. The maximum altitude in SCSV is lower than in SN, so altitudinal movements are topographically limited (Powell and Mitchell 1998). Additionally, the lower sample size of SCSV compared to SN and OM would further contribute to its lower mean home range size. Increasing the sample size and sex-ratio representativeness of GPS-collared and monitored ibexes in SCSV is required to further confirm whether the differences found were artifactual.

### Home range overlap

The lower seasonal overlaps of core areas compared to seasonal home range overlaps suggest that Iberian Ibex shift core areas within a more stable and annually constant home range. The low home range overlap detected in OM, which is the less productive study area with reintroduced ibexes, indicates low site fidelity.

This is probably linked to lower resource availability in OM, low population density, and the need to explore to localize seasonal availability of resources (Morrison et al. 2021). However, as a population reinforcement, OM ibexes should have a lower risk of dispersion than in a reintroduction scenario (Scillitani et al. 2012b).

As previously discussed, seasonal migrations in SN could explain the lower seasonal home range overlap compared to SCSV. Altitudinal migration optimizes resource exploitation and exposure to favorable weather conditions (Granados et al. 2001; Hsiung et al. 2018). As they return to previously exploited areas with predictable resources, established populations with knowledge of their home area tend to show lower seasonal home range overlap (Morrison et al. 2021), such as the Iberian Ibex population in SN. Conversely, in SCSV the lower altitudinal range restricts altitudinal movements compared to SN, increasing seasonal overlaps. Additionally, other factors contributing to higher overlap in SCSV than in SN could include interaction with sympatric ungulate species or human activities (Theuerkauf and Rouys 2008; Tablado et al. 2016), both denser and more abundant in SCSV than in SN.



**Table 6.** Generalized linear mixed model fitted for seasonal overlaps among core areas (KDE50) and home ranges (KDE95) for the Iberian Ibex (*Capra pyrenaica*).

	Estimate	SE	t	P
KDE50 overlap				
Intercept	-2.53	1.38	-1.83	0.07
Sex (males)	-2.00	0.66	-3.03	<0.001
Spring	-0.60	0.54	-1.11	0.27
Summer	-0.09	0.46	-0.19	0.85
Winter	-0.29	0.49	-0.59	0.56
Sarcoptic mange	-0.71	0.55	-1.28	0.20
KDE95 overlap				
Intercept	-1.38	1.08	-1.28	0.20
Sex (males)	-1.45	0.21	-6.85	<0.001
Spring	-0.01	0.24	-0.06	0.96
Summer	-0.09	0.24	-0.37	0.71
Winter	-0.11	0.24	-0.44	0.66
Sarcoptic mange	-0.40	0.21	-1.88	0.06

### Sarcoptic mange

The lower annual core areas of ibexes affected by sarcoptic mange are consistent with previous observations in other mammal species, such as wombats (*Vombatus ursinus*) and red foxes (*Vulpes vulpes*), for which individuals infected with sarcoptic mange experience reduced mobility—likely due to lesions, pain, and itch (Overskaug et al. 1994; Simpson et al. 2016). The impact of sarcoptic mange on home range has not been previously observed in ruminants. Despite the difference in severity of sarcoptic mange in male and female Iberian ibexes, the disease has been reported to unlink body condition from resource availability in both sexes (Carvalho et al. 2015; López-Olvera et al. 2015). Usually, home range size depends on the relation between energy requirement and resource availability (van Beest et al. 2011; Brivio et al. 2014). However, sarcoptic mange seems to disrupt this relationship, making larger core areas unnecessary for mange-affected ibexes as they are unable to improve their body condition through the search for high-quality habitats.

On the other hand, the low effect of sarcoptic mange in Iberian Ibex home ranges, coupled with the reported survival of mange-affected ibexes (Alasaad et al. 2013), indicate that Iberian Ibex spatial behavior is not severely affected by sarcoptic mange to the point of compromising individual survival of the host. This suggests the occurrence of individual and population resistance to *S. scabiei* in areas where sarcoptic mange is endemic (Pérez et al. 2022). It is possible that over time Iberian Ibex populations in these areas have developed some level of immunity or tolerance to the disease, allowing them to persist and survive despite being infected.

The comprehensive description and analysis of home ranges for the 3 Iberian Ibex populations in this study add to knowledge of environmental requirements relevant to the management and conservation of this species, particularly in the context of climate change predictions. Climate change predictions may trigger negative effects on population dynamics and the development of adaptive responses, including shifts in movements and migration (Lovari et al. 2020). Therefore, description of key areas and behaviors, identification of the most reliable methodology to estimate home range, and the contribution of new

basal data will be profitable for monitoring and characterizing changes related to global warming. The current global warming scenario, leading to more extreme and atypical environmental conditions, can affect first and more severely range-restricted species, particularly polar and mountaintop species, even causing their extinction (Parmesan 2006).

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### Supplementary data

Supplementary data are available at *Journal of Mammalogy* online.

**Supplementary Data SD1.**—Bibliographic review information.

**Supplementary Data SD2.**—Supplementary statistical results.

### Author contributions

MV and RP-R contributed equally on the development of formal analysis, and writing (original draft, and review and editing); PF: funding acquisition and investigation; RCSE, JMP, FJC-ML, PPY: conceptualization and investigation; JRL-O: conceptualization, investigation, and writing (review and editing); JEG: conceptualization, funding acquisition, investigation, supervision, and writing (original draft).

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### Conflict of interest

None declared.

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