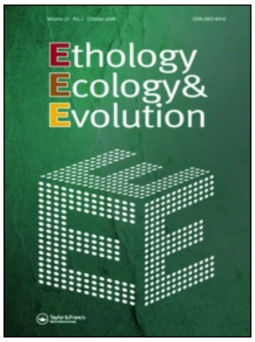

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Landscape and niche specialisation of two brush-tailed mice species *Calomyscus elburzensis* and *C. hotsoni* in Iran: a case of the role of ecological niche modelling in finding area(s) of contact

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Brush-tailed mice (family Calomyscidae) are small rodents found on the Iranian plateau and surrounding areas. To date, little discussion of the ecological aspects, habitat suitability and niche differentiation has been provided for members of this family. Herein, to model the potential distributions and describe habitat preferences of *Calomyscus elburzensis* and *C. hotsoni*, the maximum entropy modelling (MaxEnt) approach was used based on data collected through field expeditions, review of the literature and various databases. Species distribution modelling showed that minimal temperature of the coldest month and precipitation of the coldest quarter were the most important factors in predicting the distribution of *C. elburzensis*. However, occurrence of *C. hotsoni* was affected greatly by isothermality and annual precipitation. The mountainous regions in northeastern Iran, the central portions of the Elburz Mts, and the eastern hillsides of the Zagros Mts were identified as the most suitable habitats for *C. elburzensis*, whereas the western parts of South Khorasan province, the forest steppes in the southeast of Iran, and the southwestern extension of the Jebal Barez Mts in central Iran were highly suitable for *C. hotsoni*. Measurement of ecological niche overlaps showed low similarity between the niches of these two species. Nevertheless, the modelling identified areas of suitable habitat in the north centre parts of both South Khorasan and Kerman provinces where both or either of these species could occur. Moreover, *C. elburzensis* inhabited cold mountains, Mediterranean, and cold semi-desert climatic conditions, whereas *C. hotsoni* was generally showed high level of habitat suitability to hot dry desert and hot semi-desert climatic conditions. *C. elburzensis* mainly inhabits forest steppe and semi-desert biotopes, whereas *C. hotsoni* occupies

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desert lowlands in addition to forest steppe and semi-desert biotopes. Further studies are needed to resolve the distribution of each species and to follow their interactions in potential contact zones.

KEY WORDS: niche differentiation, habitat suitability, ecological niche modelling, contact zone, Rodentia, Calomyscidae.

INTRODUCTION

An ecological niche can be defined as all the resources and environmental conditions that are necessary for a species to maintain a viable population (MacArthur 1972). Each species uses an ecological niche, which may vary, often with considerable overlap, among different geographic areas, seasons, habitats, and/or food resources. The term niche differentiation is synonymous with niche segregation, niche separation or niche partitioning and all refer to the process by which natural selection drives competing species into different patterns of resource use or different niches. Spatial niche differentiation may be described as a form of habitat separation which may serve as a mechanism for species coexistence in resource-limited systems (Scott & Dunstone 2000; Zhong et al. 2016). Hence, coexistence of two species might happen through mechanisms that avoid competitive exclusion, such as resource partitioning or niche separation, especially when food resources are limited (Illoldi-Rangel et al. 2004; Holt 2009).

Small terrestrial mammals including some rodents are very poor at dispersing across altitudinal and habitat barriers, only a few miles in breadth (Bowers & Brown 1982). There is a positive relationship between the actual size and shape of the home range and body size of the animal (e.g. Kelt & Van Vuren 1999) or the productivity of food (e.g. carnivores have larger home ranges than omnivores or herbivores of similar body size; Lindstedt et al. 1986). Since rodents generally have small home ranges, it is common to observe several species which potentially interact within a relatively small geographic area (Brown 1971; Lindstedt et al. 1986; Kelt & Van Vuren 1999).

Geographic structure of contact zones influences the dynamic of the evolutionary processes (Cardozo & Chiaraviglio 2008). Morphological similarities among coexistence species suggest potential interactions that may result in niche differentiation where ecologically similar species may diverge in their landscape-scale habitat use (Cardozo et al. 2012). In contrast, competitive exclusion between closely related species is proposed to prevent range overlap and therefore could maintain parapatric distributions when species have diverged due to geographical isolation but retained the same environmental niche (niche conservatism). However, secondary contact following range expansion may result in morphological or ecological character displacement (Brown & Wilson 1956) in the contact zone where the species are in sympatry. This could result in a differentiation of their environmental niche on each side of their common boundary (Ricklefs 2010). Thus, greater differences in environmental niches in cases of sympatry are expected compared to allopatric distributions (Dayan & Simberloff 2005; Wiens & Graham 2005). All in all, species distributions result from interactions of ecological and evolutionary factors including abiotic restrictions, dispersal limitations, interspecific competitions, and local adaptations. Competitive interference is likely responsible for discontinuous distributions, local allopatry, of similar species. Hence, coexistence or local sympatry and geographical and local allopatry are of interest to systematists for a better understanding of evolutionary processes and phylogenetic inferences (Rychlik 2005).

Brush-tailed mice (family Calomyscidae, Vorontsov & Potapova 1979) are small rodents found in rocky outcrops and semi-mountainous areas in desert regions of Iran, Turkmenistan, Afghanistan, Pakistan, Azerbaijan, and Syria (Musser & Carleton 2005; Kilpatrick 2017). Goodwin's brush-tailed mouse (*Calomyscus elburzensis* Goodwin 1938) has been reported from mountains of northern and north-eastern Iran, eastern parts of the Yazd province (Iran), western Iran in Zanjan and Esfahan provinces, southwestern and southern Turkmenistan and northwestern Afghanistan (Lebedev et al. 1998; Musser & Carleton 2005; Hamidi et al. 2015, 2016; Akbarirad et al. 2016b; Kilpatrick 2017; Yusefi et al. 2019). This species is found in barren, dry and rocky habitats in mountains with Mediterranean spring rains and in other areas with cold winters and little vegetation (winters are milder at lower elevation sites). In the Elburz Mts, near the northeastern parts of its distribution, habitat has been reported as rocky outcrops with numerous cracks on steep ridges and steep mountain slopes (Hamidi et al. 2016; Shenbrot & Molur 2016; Kilpatrick 2017). Hotson's brush-tailed mouse (*C. hotsoni* Thomas 1920) has been recorded from eastern, southern and southeastern parts of Iran (including Hormozgan, Kerman and desert mountain range of Sistan and Baluchestan provinces), and southwestern regions of Pakistan (Musser & Carleton 2005; Norris et al. 2008; Khajeh et al. 2015; Kilpatrick 2017; Yusefi et al. 2019). Recently this species has been reported from the South Khorasan province, in the northeast of Iran (Akbarirad et al. 2016a; Hamidi et al. 2016). This species is found in arid rocky habitats and dry rocky mountain tops with sparse shrubby vegetation and it may be restricted to the Saharo-Sindian phylogeographic region which is characterised by hot, dry summers and mild winters (Norris et al. 2008; Kilpatrick 2017).

Taxonomic studies of Goodwin's and Hotson's brush-tailed mice have had a long history and have documented biological (Meyer & Malikov 1995, 1996; Hamidi et al. 2015, 2017, 2018), morphological (Musser & Carleton 2005; Malikov et al. 2006; Shahabi et al. 2011; Hamidi et al. 2017), molecular (Norris et al. 2008; Shahabi et al. 2013; Hamidi et al. 2016; Akbarirad et al. 2016a, 2016b) and karyological (e.g. Graphodatsky et al. 2000; Meyer & Malikov 2000; Malikov et al. 2001; Shahabi et al. 2010) differences. In contrast, very little is known of their habitat, ecological requirements and interactions either in the wild or in captivity (e.g. Lay 1967; Habibi 1977; Nowak 1999; Hamidi et al. 2016, 2018) and no studies have been conducted to compare the habitats used by these two species.

In this study, we aimed to describe the potential distribution and habitat suitability and to determine possible niche overlap between these two species of brush-tailed mice. A maximum entropy modelling (MaxEnt) approach was used to construct potential distribution maps based on presence data and climatic variables (Phillips et al. 2006). Environmental niche modelling, also known as ecological niche modelling, species distribution modelling, predictive habitat distribution modelling, and climate envelope modelling has allowed advances in the knowledge of geographic ecology of species, ecological and evolutionary determinants of spatial patterns of biodiversity and detects areas of endemism, range shifts in response to climate change, as well as inferences of speciation processes and species delimitation (Elith et al. 2006; Rissler & Apodaca 2007; Elith & Leathwick 2009). The known distribution of Goodwin's and Hotson's brush-tailed mice has been expanded greatly in the past 15 years (Kilpatrick 2017; Yusefi et al. 2019); thus, use of ecological niche modelling will characterise the niche of these two species to predict other areas where these two taxa may occur.

In general, these two species are similar in their external morphology (general body size and phenotypic characteristics), as well as their nesting habits and preferred habitats (Hamidi et al. 2016; Kilpatrick 2017). It is hypothesised that resource partitioning or interspecific interactions would occur where they coexist. Although no areas of contact are currently known, these two species have been reported to occur at localities less than approximately 100 km apart in the northern parts of South Khorasan province in Iran. Due to close approximation of the southern extension of the range of *C. elburzensis* and northern extension of the range of *C. hotsoni*, similarities observed in the landscape of these two areas, and the absence of any obvious potential geographic barrier, it is likely that these two species may be found in contact or may have occurred in contact in the past or even may occur in contact in the future in this region of Iran.

MATERIALS AND METHODS

Study area

Sampling area was located in eastern Iran (25–38°N and 55–63°E), which is an ideal region for the study of landscape-scale niche differentiation of small rodents because of the documented diversity with 30 species of rodents (Darvish & Rastegar-Pouyani 2012; Hamidi et al. 2016) including members of the Calomyscidae. Eastern Iran is located in the arid belt and is separated from other regions of Iran by topographic barriers such as Kopet-Dag Mts ranging to the north and two large deserts, Dasht-e-Lut to the south and Central Kavir to the west (Darvish & Rastegar-Pouyani 2012). Heights in the eastern parts of Iran consist of numerous chains of mounts: (1) Binalud-Ala-Dag heights as an eastern extension of Elburz Mts mainly located in North Khorasan province, (2) southern extension of Kopet-Dag Mts with its main heights, Hezar Masjed-Allāho Akbar located in northeastern most part of Iran, (3) Chehel Tan Mts and Khaje-Morad heights in the centre of Razavi Khorasan province, (4) toward the west, heights include Shirkuh Mts located in the centre of Iran, south of Yazd province, and Jebal Barez Mts in Kerman province, (5) Bon-Dar Mts with the Darmian heights in the east and Bagheran Mts with two main heights named Ark, and Shadan and Olang in the west which are in South Khorasan province, (6) Taftan Mts in the southeastern most part of Iran near the Iran-Pakistan border, and (7) Bashagard heights southwest of Taftan toward the south extension of Zagros Mts (Darvishzadeh 2003; Aghanabati 2004).

The climatic conditions in eastern Iran include Mediterranean with spring rains, cold mountains, cold semi-desert, hot semi-desert, dry desert, hot dry desert and coastal dry areas, with a variety of biotopes such as forest steppe, forest and woodland, semi-desert and desert lowland (Islamic Republic of Iran Meteorological Organization Site, at http://www.irimo.ir). In the northeast, winters are relatively cold with medium snowfall (average annual precipitation is only 277 mm in areas with greater humidity). Spring and fall are mild, while summers are relatively dry and hot. The typical vegetation of northeast Iran is Greek juniper (Cupressaceae; *Juniperus excelsa* M. Bieb.), Mount Atlas pistache (Anacardiaceae; *Pistacia atlantica* Desf.), dog rose (Rosaceae; *Rosa canina* L.), sun spurge (Euphorbiaceae; *Euphorbia helioscopia* L.), shrubby horsetail (Ephedraceae; *Ephedra* sp.) and berberry shrubs (Berberidaceae; *Berberis integerrima* Bunge) as well as cover of blessed milk thistle [Asteraceae; *Silybum marianum* (L.) Gaertn.], and harmel peganum (Zygophyllaceae; *Peganum harmala* L.). In southeastern Iran, winters are mild, and summers are very hot. Sparse shrubby vegetation is typical, consisting mainly of bushes of shrubby horsetail, common oat (Poaceae; *Avena sativa* L.), Mount Atlas pistache and dwarf mazari palm [Arecaceae; *Nannorrhops ritchieana* (Griff.) Aitch.]. Generally, the vegetation was denser at higher latitudes and sparser at lower latitudes in the eastern parts of Iran (Hamidi et al. 2016).

Field work and trapping method

Trapping sessions were performed during January 2013 and April 2018 using custom-made mesh live traps baited with suitable food types. Trapping was carried out for 39 trials (approximately 1000 trap-nights). Traps were set in the late afternoons and checked initially in the following mornings. Date, sex, body weight and approximate age of all captured individuals were recorded. Plant coverage, elevation, climatic conditions, geographical and environmental variables, geological and geomorphological features such as soil type, and overall habitat structure were also recorded for each sampling locality during field expeditions. Data on burrow and feeding signs of the rodents were also collected.

In total, six rocky areas and 36 trapping stations in eastern Iran were monitored in this study based on previous findings on the preferred habitat types, geological zones and soil structures used by brush-tailed mice. Due to insufficient records from northeastern parts of the distribution range of *C. elburzensis* in Iran, near the Iran-Turkmenistan border, and also northern most extension of the distribution range of *C. hotsoni*, these localities were selected for sampling (identified in Table 1 as Hamidi et al. 2016, 2017; K. Hamidi unpublished data). These areas included the Binalud-Ala-Dag heights (2 stations; 6 *C. elburzensis* captured), Hezar Masjed- Allāho Akbar heights (9 stations; 6 *C. elburzensis* captured) (Fig. 1A-B), Khaje-Morad heights (6 stations; 48 *C. elburzensis* captured), Darmian heights (4 stations; no *Calomyscus* captured), Bagheran Mts (10 stations; 5 *C. hotsoni* captured) (Fig. 1C-D), and finally, Taftan Mts (5 stations; 1 *C. hotsoni* captured).

In total, 60 individuals of *C. elburzensis* and 6 of *C. hotsoni* were captured. Captured brush-tailed mice were examined for any signs of diseases and overall welfare before being transferred to the animal house where each was kept in a separate cage to ensure their good health before further experiments such as mating trials. They were maintained in captivity for different investigations including biological (K. Hamidi unpublished data), developmental (Hamidi et al. 2017), and behavioural studies in captivity (Hamidi et al. 2018). Some of them were released in their home range when the project was finished.

Species identification was carried out based on morphological and morphometric characters using identification keys and distinguishing characteristics (Corbet 1978; Etemad 1984; Kilpatrick 2017), and also molecular studies (Table 1). Specimens were deposited in the Research Group of Rodentology, Ferdowsi University of Mashhad, Iran. Animal care and experimental procedures were performed in compliance with the "Guideline for the care and use of laboratory and experimental animals, Rodentology Research Group, Ferdowsi University of Mashhad".

Data collection and point localities

Distribution data (collecting locality coordinates) for these two species of brush-tailed mice were obtained from available literature records (Hassinger 1973; de Roguin 1988; Graphodatsky et al. 2000; Norris et al. 2008; Shahabi et al. 2010; Akbarirad et al. 2015, 2016a, 2016b; Khajeh et al. 2015; Hamidi et al. 2016, 2017; Safapour 2017; Haddadian Shad & Darvish 2018a, 2018b), and databases (https://www.gbif.org/ and http://www.vertnet.org/). A total of 65 and 22 localities of presence were identified for *C. elburzensis* and *C. hotsoni*, respectively (Table 1).

Modelling of species distribution and landscape analyses

Environmental variables predictors including 19 bioclimatic layers (Bio1-19) obtained from the WorldClim database (http://www.worldclim.org/) were used as independent variables. All layers were downloaded as 30 arc-second (~ 1 km) resolution, and then cropped using ArcGIS v. 10.3 (ESRI) to include Iran, Turkmenistan, Afghanistan and Pakistan boundaries. Environmental layers

Table 1.

Coordinate records for two species of brush-tailed mice, *Calomyscus elburzensis* and *C. hotsoni*, used in the present study.

No.	Longitude	Latitude	Locality	Museum/NCBI Accession No.	Reference(s)
Goodwin's brush-tailed mouse (*C. elburzensis*)					
1	60.88	36.25	Aghdarband; Sarakhs; Razavi Khorasan; Iran	KT884549 ZMFUM1921	Akbarirad et al. 2016b
2	58.72	37.43	Tandure; Dargaz; Razavi Khorasan; Iran	KT884548 ZMFUM1675	Akbarirad et al. 2016b
3	59.57	36.25	Khaje Morad; Mashhad; Razavi Khorasan; Iran	KT878581 ZMFUM1542	Akbarirad et al. 2016b
4	54.32	31.66	Fakhr Abad; Yazd; Iran	KT878582 ZMFUM171	Akbarirad et al. 2016b
5	61.12	36.50	Aghdarband; Sarakhs; Razavi Khorasan; Iran	KT878585 ZMFUM1874	Akbarirad et al. 2016b
6	57.29	37.49	Dasht; Bojnord; North Khorasan; Iran	KT884579 ZMFUM1933	Akbarirad et al. 2016b
7	60.40	35.15	Shahneshin Mts; Nasr Abad; Torbat-e Jam; Razavi Khorasan; Iran	KT878587 ZMFUM2088	Akbarirad et al. 2016b
8	58.86	36.36	Soghand; Binalud Mts; Neyshabour; Razavi Khorasan; Iran	KT884550 ZMFUM2148	Akbarirad et al. 2016b
9	58.41	36.35	Buzhan; Binalud Mts; Neyshabour; Razavi Khorasan; Iran	KT884551 ZMFUM2152	Akbarirad et al. 2016b
10	58.17	34.40	Siahkuh; Bajestan; South Khorasan; Iran	KT884552 ZMFUM2195	Akbarirad et al. 2016b
11	57.37	37.42	Kurkhud; Bojnord; North Khorasan; Iran	KT878590 ZMFUM3533	Akbarirad et al. 2016b
12	57.90	37.34	Salook; Esfaraien; North Khorasan; Iran	KT878588 ZMFUM2978	Akbarirad et al. 2016b
13	59.91	33.60	Shaskooh; Hajiabad; Ghaen; South Khorasan; Iran	KT884554 ZMFUM3305	Akbarirad et al. 2016b
14	60.11	33.04	Darmiyan; Birjand; South Khorasan; Iran	KT884558 ZMFUM4530	Akbarirad et al. 2016b
15	60.22	32.99	Gezik; Birjand; South Khorasan; Iran	KT884557 ZMFUM4529	Akbarirad et al. 2016b
16	57.18	36.52	Zarghan; Sabzevar; Razavi Khorasan; Iran	KT884556 ZMFUM4490	Akbarirad et al. 2016b
17	54.10	31.71	Fakhr Abad; Yazd; Iran	KT878584 ZMFUM1777	Akbarirad et al. 2016b

(*Continued*)

Table 1.

(*Continued*)

No.	Longitude	Latitude	Locality	Museum/NCBI Accession No.	Reference(s)
18	59.49	36.94	Kopet-Dag Mts; Kalat; Razavi Khorasan; Iran	KY039480 ZMFUM5014	Hamidi et al. 2017
19	59.57	36.25	Khaje Morad; Mashhad; Razavi Khorasan; Iran	KT884547	Akbarirad et al. 2016a
20	48.59	36.12	Qeydar; Zanjan; Iran	ZMFUM3925	Akbarirad et al. 2016b
21	48.59	37.12	Qeydar; Zanjan; Iran	ZMFUM3937	Akbarirad et al. 2016b
22	51.77	33.45	Karkas; Isfahan; Iran	ZMFUM3938	Akbarirad et al. 2016b
23	59.69	36.14	Khaje Morad; Mashhad; Razavi Khorasan; Iran	ZMFUM5019	K. Hamidi unpublished data
24	59.69	36.14	Khaje Morad; Mashhad; Razavi Khorasan; Iran	ZMFUM5022	K. Hamidi unpublished data
25	54.08	31.65	Esmaeilieh; Yazd; Iran	ZMFUM1780	Haddadian Shad & Darvish 2018a
26	59.9	33.6	Bajestan; South Khorasan; Iran	ZMFUM2195	Haddadian Shad & Darvish 2018a
27	58.71	33.92	Barz Abad; Ghaen; South Khorasan; Iran	ZMFUM5048	Safapour 2017
28	57.43	37.93	Salook; Esfaraien; North Khorasan; Iran	-	Akbarirad et al. 2015
29	54.15	31.65	Shirkuh Mts; Cheshme; Taft; Yazd; Iran	-	Akbarirad et al. 2016b
30	54.08	31.64	Shirkuh Mts; Ab-Mazrae; Taft; Yazd; Iran	-	Akbarirad et al. 2016b
31	54.08	31.65	Shirkuh Mts; Dare-Bidun; Taft; Yazd; Iran	-	Akbarirad et al. 2016b
32	57.16	37.16	Salook; Esfaraien; North Khorasan; Iran	-	Akbarirad et al. 2015
33	54.42	31.41	Kuhe Bakhtaki; Mehriz; Yazd; Iran	-	Akbarirad et al. 2016b
34	56.52	37.44	Kurkhud; Bojnord; North Khorasan; Iran	-	Akbarirad et al. 2016b

(*Continued*)

Table 1.

(*Continued*)

No.	Longitude	Latitude	Locality	Museum/NCBI Accession No.	Reference(s)
35	58.53	37.36	Agh Mazar Abad; Maneh and Samalqan; North Khorasan; Iran	-	Graphodatsky et al. 2000
36	54.12	31.55	Godar Nir; Yazd; Iran	-	Haddadian Shad & Darvish 2018b
37	54.06	31.65	Cheshmeh Piazi; Yazd; Iran	-	Haddadian Shad & Darvish 2018b
38	54.41	31.4	Mehriz; Yazd; Iran	-	Haddadian Shad & Darvish 2018b
39	54.1	31.7	Ta Mehr; Yazd; Iran	-	Haddadian Shad & Darvish 2018b
40	57.93	37.33	Gelian; North Khorasan; Iran	-	Shahabi et al. 2010
41	58.79	35.51	Kashmar; Razavi Khorasan; Iran	-	GBIF/VertNet
42	58.41	36.87	Quchan; Razavi Khorasan; Iran	-	GBIF/VertNet
43	54.34	35.89	Semnan; Semnan; Iran	-	GBIF/VertNet
44	59.53	36.91	Kopet-Dag Mts; Cheshme-Kabkan; Kalat; Razavi Khorasan; Iran	-	K. Hamidi unpublished data
45	59.35	36.91	Kopet-Dag Mts; Kaj-Darre; Kalat; Razavi Khorasan; Iran	-	K. Hamidi unpublished data
46	59.35	37.12	Tirgan; Dargaz; Razavi Khorasan; Iran	-	K. Hamidi unpublished data
47	59.36	37.09	Robat; Kalat; Razavi Khorasan; Iran	-	K. Hamidi unpublished data
48	57.2	37.36	Gachranlo; Bojnord; North Khorasan; Iran	-	(VG. Malikov, personal communication)
49	56.51	37.43	Kurkhud; Bojnord; North Khorasan; Iran	-	(VG. Malikov, personal communication)
50	56.71	37.44	Darekesh; Bojnord; North Khorasan; Iran	-	(VG. Malikov, personal communication)
51	64.43	33.54	25 mi E Maimana, Fariab, Afghanistan	FMNH102973	Hassinger 1973

(*Continued*)

Table 1.

(*Continued*)

No.	Longitude	Latitude	Locality	Museum/NCBI Accession No.	Reference(s)
52	62.1	34.2	8 mi N Herat, Herat, Afghanistan	FMNH102977	Hassinger 1973
53	63.1	34.57	68 mi by road E Herat, Zarmast (Sauzak) Pass, Afghanistan	FMNH201980	Hassinger 1973
54	58.08	37.91	Fir'uza (14 km SW Ashgabat), Central Kopet-Dag, Turkmenistan	-	Graphodatsky et al. 2000
55	58.06	38.03	Chuli (36 km W Ashgabat), Central Kopet-Dag, Turkmenistan	-	Graphodatsky et al. 2000
56	58.83	37.75	Kalininsk, Central Kopet-Dag, Turkmenistan	-	Graphodatsky et al. 2000
57	57.43	38.38	5 km S Bakharden, Central Kopet-Dag, Turkmenistan	-	Graphodatsky et al. 2000
58	58.71	37.81	G'aurs (36 km E Ashgabat), Central Kopet-Dag, Turkmenistan	-	Graphodatsky et al. 2000
59	59.61	37.35	Archenyan, Eastern Kopet-Dag, Turkmenistan	-	Graphodatsky et al. 2000
60	61.25	35.91	Akar-Chashme, Western Badkhyz, Turkmenistan	-	Graphodatsky et al. 2000
61	58.16	37.83	Summit Mt Dushak, Central Kopet-Dag, Turkmenistan	-	Graphodatsky et al. 2000
62	56.5	38.33	Ai-Dere, Western Kopet-Dag, Turkmenistan	-	Graphodatsky et al. 2000
63	56.28	38.96	Gyzylarbat, Western Kopet-Dag, Turkmenistan	-	Graphodatsky et al. 2000
64	55.66	39.16	Danata, Western Kopet-Dag, Turkmenistan	-	Graphodatsky et al. 2000
65	54.83	39.11	Little Balkhan Mountain, Turkmenistan	-	Graphodatsky et al. 2000
Hotson's brush-tailed mouse (*Calomyscus hotsoni*)					
66	58.69	32.92	Tejg; Ark heights; Birjand; South Khorasan; Iran	KY039482 ZMFUM5025	Hamidi et al. 2017
67	58.91	32.41	Hamech; Shadan and Olang heights; Birjand; South Khorasan; Iran	KY039483 ZMFUM5026	Hamidi et al. 2017
68	61.77	27.30	Birk Mts; Paskooh; Saravan; Sistan and Baluchestan; Iran	KT884560	Akbarirad et al. 2016a

(*Continued*)

Table 1.

(*Continued*)

No.	Longitude	Latitude	Locality	Museum/NCBI Accession No.	Reference(s)
69	61.17	28.15	Abkhan Mts; Khash; Sistan and Baluchestan; Iran	KT884567	Akbarirad et al. 2016a
70	59.21	32.81	Bagheran Mts; Birjand; South Khorasan; Iran	KT884573	Akbarirad et al. 2016a
71	60.78	29.74	Malek Siahkuh Mts; Zahedan; Sistan and Baluchestan; Iran	KT884568	Akbarirad et al. 2016a
72	61.46	27.18	Saravan; Sistan and Baluchestan; Iran	ZMFUM 2102	Shahabi et al. 2010
73	58.86	32.44	Gound; Nehbandan; South Khorasan; Iran	ZMFUM5027	K. Hamidi unpublished data
74	57.24	30.04	Jupar; Kerman; Iran	MHNG1686.72	de Roguin 1988
75	57.19	29.33	Zahrud-e Bala; Kerman; Iran	MHNG1686.73	de Roguin 1988
76	61	28.34	Kusheh; Sistan and Baluchestan; Iran	MHNG1686.74	de Roguin 1988
77	57.49	26.50	Fanuj; Sistan and Baluchestan; Iran	-	Khajeh et al. 2015
78	58.04	28.60	Anbar Abad; Kerman; Iran	-	Khajeh et al. 2015
79	59.64	26.55	Kohe Heydar; Sardasht; Bashagard; Hormozgan; Iran	-	Khajeh et al. 2015
80	60.85	29.51	Zahedan; Sistan and Baluchestan; Iran	-	GBIF/VertNet
81	60.36	26.39	Nikshahr; Sistan and Baluchestan; Iran	-	GBIF/VertNet
82	61.25	28.35	Khash; Sistan and Baluchestan; Iran	-	GBIF/VertNet
83	65.84	28.02	6 km E Wadh; Dancer; Khuzdar; Baluchestan; Pakistan	EU135583	Norris et al. 2008
84	64.15	26.76	Mitha Singh; Panjgur; Baluchestan; Pakistan	EU135579	Norris et al. 2008
85	66.88	26.38	Rani Kot; near Shergart Fort; Dadu; Sindh; Pakistan	EU135582	Norris et al. 2008
86	66.83	26.73	35 km W Dadu; Sindh; Pakistan	UF15092	Norris et al. 2008
87	64.09	26.96	Panjgur; Gwambuk; Pakistan	FMNH83058	GBIF/VertNet

ZMFUM: Zoology Museum of Ferdowsi University of Mashhad; FMNH: Field Museum of Natural History (Chicago, IL); MHNG: Muséum d'Histoire Naturelle de Genève; UF: University of Florida, Museum of Natural History. Data available on the web: NCBI at https://www.ncbi.nlm.nih.gov/, GBIF at https://www.gbif.org/, and VerNet at http://www.vertnet.org/

Fig. 1. — (A) Goodwin's brush-tailed mouse (*Calomyscus elburzensis*). (B) Habitat and vegetation cover of *C. elburzensis* in the Hezar Masjed-Allāho Akbar heights, Razavi Khorasan province. (C) Hotson's brush-tailed mouse (*Calomyscus hotsoni*). (D) Habitat and vegetation cover of *C. hotsoni* in the Shadan and Olang heights, Bagheran Mts, South Khorasan province.

and records were applied in OpenModeller v. 1.0.7 (de Souza Muñoz et al. 2011) to obtain the relevant grid values for each record.

A multi-collinearity test was conducted using Pearson correlation coefficient (r) in SPSS v. 16.0 (SPSS Inc. 2007) to identify the variables with correlations greater than 0.75. Variables with correlations lower than 0.75 were chosen for inclusion in species distribution models (Table 2).

Maximum entropy modelling (MaxEnt v. 3.3.3e) (Phillips et al. 2006) was employed to assess the environmental factors at localities where these two species of brush-tailed mice occur and to predict suitable regions for the presence of these species. Ten per cent of the data were used as test data and the rest were considered as training data. Maximum number of iterations of 500 with a 0.00001 convergence threshold and a multiplier regularisation of 1 were used for running models. MaxEnt was run 10 times for each species in order to obtain averages of predictions (Phillips et al. 2006). The area under receiver-operating-characteristic curves (AUCs) was considered as the criterion for model accuracy and acts as a measure for the model's discrimination ability to indicate present points from absent ones in a procedure that is independent from suitability thresholds (Elith et al. 2011). The value of AUC ranges between 0 and 1. A model with no predictive ability should return an AUC of 0.5; an AUC greater than 0.5 indicates that the model is better than random; and a value close to 1 indicates near-perfect accuracy of the model (Phillips & Dudík 2008).

ENMTools v. 1.0 was also used to examine Schoener's D statistic for calculating niche overlap among the two species (Warren et al. 2010). ASCii files for each species obtained from MaxEnt analysis were applied in ENMTools for computing the niche overlap. The value of Schoener's D index ranges between 0 and 1, in which the value of 0 means that ecological niches do not have any overlap, and values close to 1 indicate high similarity between ecological niche models and hence, the ecological niches are considered as identical (Schoener 1968).

Table 2.

Bioclimatic variables used to develop the distribution models for Goodwin's brush-tailed mouse (*Calomyscus elburzensis*) and Hotson's brush-tailed mouse (*C. hotsoni*) in MaxEnt.

Variable	Percentage contribution value		Permutation importance (%)	
	C. elburzensis	*C. hotsoni*	*C. elburzensis*	*C. hotsoni*
Bio2 (annual mean diurnal range)	8.78	0.05	8.6	1.58
Bio3 (isothermality)	–	55.52	–	16.03
Bio4 (temperature seasonality)	0.68	2.99	2.02	17.94
Bio5 (max temperature of warmest month)	–	–	–	–
Bio6 (min temperature of coldest month)	48.22	8.95	49.41	4.15
Bio8 (mean temperature of wettest quarter)	4.45	–	2.11	–
Bio9 (mean temperature of driest quarter)	–	1.22	–	10.12
Bio12 (annual precipitation)	0.46	23.58	3.56	34.32
Bio14 (precipitation of driest month)	–	–	–	–
Bio15 (precipitation seasonality)	–	0.14	–	0.59
Bio18 (precipitation of warmest quarter)	11.35	2.42	7.22	12.77
Bio19 (precipitation of coldest quarter)	26.06	5.13	27.08	2.5

Contribution ratio (%) and permutation importance values for each layer are also shown.

RESULTS

A total of 12 layers of bioclimatic variables were selected to run the model in MaxEnt (Table 2). The mean AUC value for testing data was 0.896 ± 0.0491 for *C. elburzensis* and 0.9201 ± 0.0329 for *C. hotsoni*. The minimal temperature of the coldest month with a percentage contribution value (PC) of 48.22% and permutation importance value (PIMP) of 49.41%, and the precipitation in the coldest quarter (PC = 26.06%, PIMP = 27.08%) had the greatest effects on the final model for *C. elburzensis*. However, the niche model for *C. hotsoni*, was affected greatly by isothermality (PC = 55.52%, PIMP = 16.03%) and annual precipitation (PC = 23.58%, PIMP = 34.32%).

The niche modelling showed that the highest probability for the presence of *C. elburzensis* was in environments with the precipitation of the coldest quarter between 70 and 90 mm. However, the niche model for *C. hotsoni*, identified areas with annual precipitation between 100 and 200 mm as the most suitable ones. Moreover, with increasing the isothermality values, the probability of the presence of this species decreased.

According to the maps generated, northeastern Iran (Binalud-Ala-Dag heights, Kopet-Dag Mts and Hezar Masjed-Allāho Akbar heights, as well as heights in central Razavi Khorasan), central parts of the Elburz Mts, and eastern parts of Zagros Mts (especially northern parts of Jebal Barez Mts in Kerman province) were identified as the most suitable habitats for *C. elburzensis* (Fig. 2), whereas only forest steppes in the

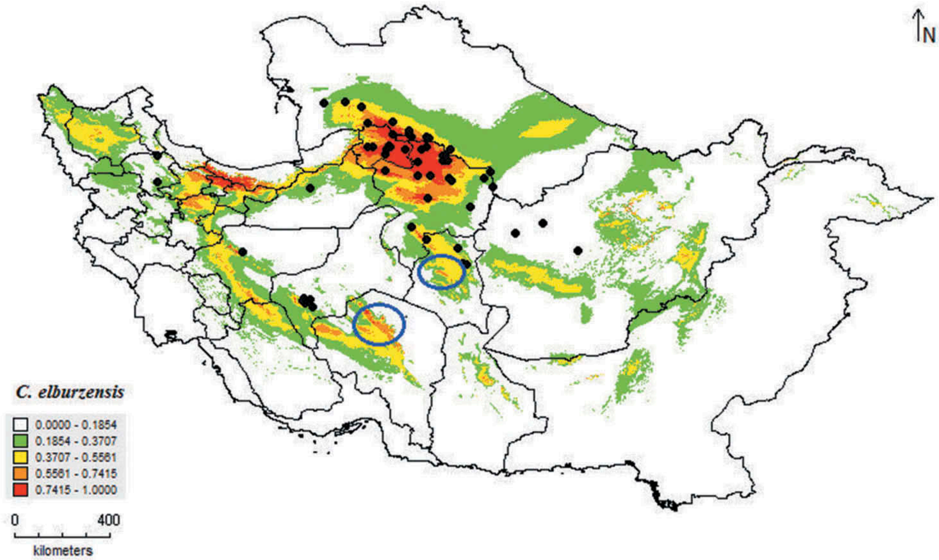

Fig. 2. — Potential distribution map of *Calomyscus elburzensis*. Known localities for *C. elburzensis* and possible contact zones for *C. elburzensis* and *C. hotsoni* are shown as black dots and blue circles, respectively.

southeastern Iran (Sistan and Baluchestan province) were predicted as the most suitable habitats for *C. hotsoni* (Fig. 3). Furthermore, the Jebal Barez Mts in central Iran (north centre of the Kerman province) and areas of north centre of the South Khorasan province were considered as possible contact zones for these two species and areas where they might be found in sympatry (Figs 2–3).

However, the Schoener's D metric value was calculated as 0.299631 which indicated that these two species show a low similarity between their ecological niches.

DISCUSSION

Species distribution models generally reveal the realised ecological niche of a species and describe the environmental conditions in which a species is able to survive and reproduce in the presence of biotic interactions, such as predation and symbiosis (Hutchinson 1957; Elith et al. 2006; Rissler & Apodaca 2007; Elith & Leathwick 2009). Since recently evolved lineages often cannot be readily recognised using traditional species criteria (concepts), a diversity of approaches has been used for species delineation (e.g., fixed or non-overlapping differences in morphological, behavioural, and ecological characters, levels of molecular divergence, reciprocal monophyly or geographic isolation) (e.g. see Blair et al. 2013; Braz et al. 2018). Thus, ecological niche modelling offers a great potential for detecting ecologically mediated parapatric speciation, when the environmental gradient variables driving speciation are included in the ecological niche modelling (de Queiroz 1998).

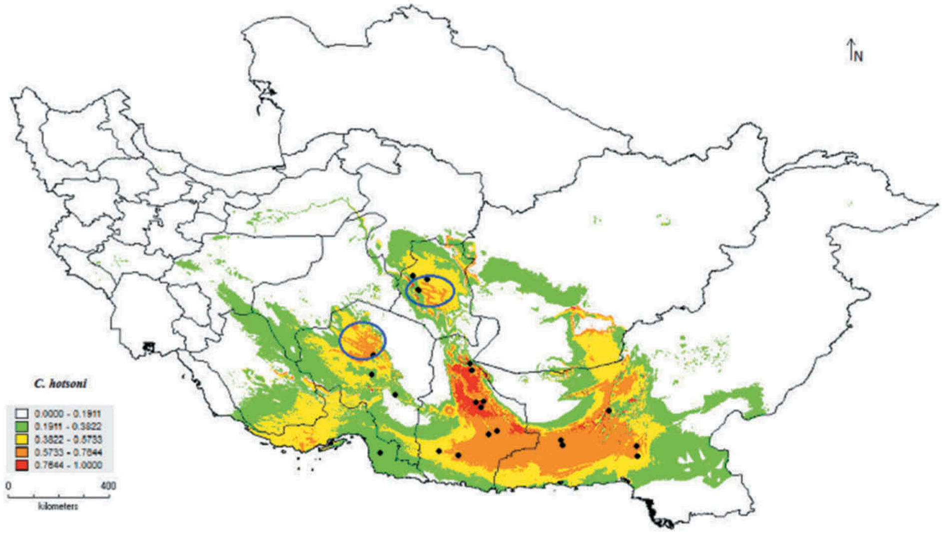

Fig. 3. — Potential distribution map of the *Calomyscus hotsoni*. Known localities for *C. hotsoni* and possible contact zones for *C. hotsoni* and *C. elburzensis* are shown as black dots and blue circles, respectively.

Distribution range and habitat suitability

The ecological niche models identified suitable climatic condition for *C. elburzensis* to occur mainly in the mountainous and higher regions of northern, northeastern and central Iran whereas the climatic conditions for the occurrence of *C. hotsoni* were found in the hot and dry regions of southeastern Iran. The predictive habitat distribution model for *C. hotsoni* suggests that suitable habitats extend from the southeastern most parts of Iran, near the type locality of the Hotson's brush-tailed mouse in southwestern Pakistan, northward to the western parts of the South Khorasan province and the southwestern extension of the Jebal Barez Mts in the Kerman province. The Central Kavir and Dasht-e-Lut are geographic barriers to the dispersal of both species. *C. elburzensis* are connected by habitats north of the Central Kavir, whereas regions east and west of the Dasht-e-Lut inhabited by *C. hotsoni* are connected by habitats south of the Dasht-e-Lut.

Goodwin's brush-tailed mouse is distributed in the Elburz Mts, Binalud-Ala-Dag heights, Kopet-Dag Mts, Chehel Tan Mts and Bon-Dar Mts in the northeast, Shirkuh and Jebal Barez Mts in central Iran, and towards west Karkas and Ghaflankooh, whereas *C. hotsoni* has been recorded from the Bagheran and Taftan Mts and the Bashagard heights in the southeast Iran (see Hamidi et al. 2016 for more details). According to the tectonic map of Iran (Fig. 4), Goodwin's brush-tailed mice were generally distributed in the Kopet-Dag-Hezar Masjed, Binalud, Elburz-Azarbijan, and Central Iran structural zones, with a variety of climates including cold mountain, Mediterranean, cold semi-desert, and marginally in hot semi-desert. Hotson's brush-tailed mice, however, were found primarily in the Flysch and Central Iran structural zones, with great habitat suitability in hot dry desert, hot semi-desert and marginally in cold semi-desert climatic conditions. *C. elburzensis* mainly inhabits in forest steppe,

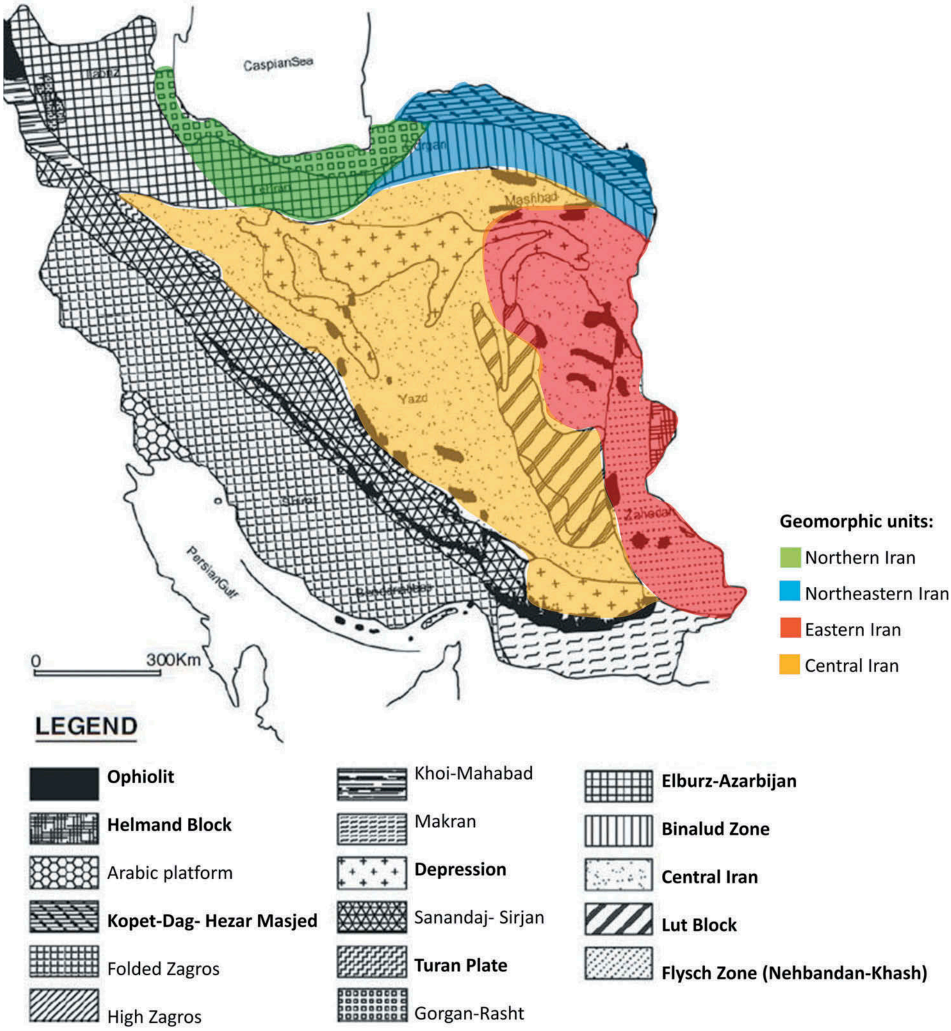

Fig. 4. — Tectonic map of Iran with approximate borders of four main geomorphic units in eastern and central Iran. Structural zones (also known as geomorphotectonic units) throughout Iran are shown in the map and listed in the legend; those which are indicated in bold are located in the four geomorphic units (reproduced from Nabavi 1976).

forests and woodlands, and semi-desert biotopes, whereas *C. hotsoni* occupies forest steppe, semi-desert biotopes, and desert lowlands. These findings are in agreement with previous findings reported by Hamidi et al. (2016).

According to the predictive habitat distribution model, suitable areas for *C. elburzensis* to occur were identified within the Irano-Turanian floristic region which mainly consists of different types of steppe coniferous and flowering plants such as *Juniperus* L. and *Pistacia* L., and also shrubs genera *Prunus* L., *Quercus* L., and *Astragalus* L., whereas predicted distribution for *C. hotsoni* was mainly located within the Sudanian floristic region with the lower plant diversity and low growing rate plant species, a coverage of flowering and small spiny trees and also shrubs such as *Prosopis* L., *Tamarix* L., *Cyperus* L., and *Acacia* (Martius 1829) (Zohary 1973; Noroozi et al. 2008). Dominant plant forms of predicted suitable habitats for *C. elburzensis* included *Juniperus* steppe forest remnants, *Pistacia-Amygdalus* steppe forest and *Artemisia* steppe, whereas for *C. hotsoni, Pistacia-Amygdalus* steppe forest, Saharo-Sindian *Acacia* steppe forest and *Artemisia* steppe were identified as dominant vegetation forms (see Zohary 1973; Noroozi et al. 2008 for vegetation characteristics and classification).

Iran has been divided into several geomorphic units, each characterised by a relatively unique record of magmatic activities, metamorphisms, tectonics, orogenic events, stratigraphy, and overall geological appearance (see tectonic maps of Iran in Stocklin & Nabavi 1973; Nabavi 1976; Alavi-Naini 1983; Aghanabati 2004). According to the niche modelling maps, suitable habitats for *C. elburzensis* are mainly located in Northeastern Iran, Northern Iran and along the western border of Central Iran geomorphic units, whereas habitat suitability for *C. hotsoni* is coincident with the Eastern and Central Iran geomorphic units (Fig. 4). The Northeastern Iran (Kopet-Dag) geomorphic unit was covered with a vast continental shelf sea during the Middle Jurassic and is composed of a thick sequence of marine and continental sediments with no reports of major sedimentary gap or volcanic activities. The Elburz range is located in Northern Iran geomorphic unit which is characterised by the dominance of platform-type sediments. The Binalud zone is a continuation of the Elburz range, located east of that range but has features comparable to those of Central Iran geomorphic unit, where rocks of all ages and several episodes of metamorphism and magmatism can be recognised. Finally, the Eastern Iran geomorphic unit is divided into two parts: Lut Block and Flysch or coloured mélange of Zabol-Baluch Zone (also called Nehbandan-Khash Band). The Lut Block is the main body of the Eastern Iran geomorphic unit, located to the west of the Flysch Zone and consists of schists overlain by limestone and other sedimentary rocks. The Flysch Zone is located between the Lut Block to the west and Helmand (near Iran–Afghanistan border) to the east. In contrast to Lut Block, the Flysch Zone is highly deformed and tectonised; most rock units in this zone are flyschoid sediments, volcanic, volcano-sedimentary, and intrusive rocks (Ghorbani 2013) (Fig. 4).

Geological and geomorphological conditions (such as soil type and hardness, soil moisture content, metamorphism, and stratigraphy), climatic conditions (such as temperature, precipitation and humidity), vegetation cover and density, dominant plants, and overall habitat structure and macro-ecological conditions are different among these rocky areas inhabited by these two species of brush-tailed mice and likely contributes to the different habitat requirements of these two species.

Contact zone and niche overlap

While *C. elburzensis* and *C. hotsoni* both inhabit a wide range of environmental conditions throughout their ranges and show little spatial overlap, probable contact zones have been identified in northern centre of both South Khorasan and Kerman provinces. In the two areas of potential contact, climatic conditions were mainly identified as hot semi-deserts and cold semi-deserts, with forest steppe and semi-desert biotopes including *Pistacia-Amygdalus* steppe forest and *Artemisia* steppe as the dominant vegetation forms. The geographic distribution of these two species in Iran is potentially parapatric based on the proximity of the ranges of the two species, the homogeneous habitat separating the two, and the lack of an apparent geographic barrier. Niche modelling analyses showed that these two species do not have a high degree of niche similarities. Hence, it would be hypothesised that this is the evolutionary outcome of *C. hotsoni* being in a southern clade which likely evolved in hotter and dry climates, whereas *C. elburzensis* is part of a northern clade that evolved in milder climates. Although these two species do not occupy very similar regions, their niches would have to be much more similar in the areas with suitable climatic conditions and plant coverage for both. Moreover, making a case that the niche separation between these two species would be much reduced in the areas of contact, where there is high suitability for both to occur, is the key to lead into the inclusion of the competition interaction.

Habitat heterogeneity and productivity

Habitat structure and primary productivity have important effects on the diversity of animal communities (MacArthur 1964; Rosenzweig 1995). In more productive habitats, the greater plant coverage, variety in vegetation cover and plant productivity influence the species diversity of small mammals (Brown & Lieberman 1973; Abramsky & Rosenzweig 1984; Wang et al. 1999). Greater plant resources, as indexed by plant coverage, may influence the complexity of habitat structure and would support greater species diversity, compared with poor habitats with sparse vegetation (Reed et al. 2006; Zhong et al. 2016).

Recently, molecular analyses of *Cytb* and *COI* gene sequences have recovered four subclades of *C. elburzensis* in northeast of Iran (Akbarirad et al. 2016b). A similar study recovered only two subclades of *C. hotsoni* in southeastern Iran (Akbarirad et al. 2016a). According to our niche modelling and our previous findings (Hamidi et al. 2016), great differences in the climatic conditions, geological characteristics, vegetation cover and overall habitat structure were observed among areas inhabited by *C. elburzensis* in Iran, and populations of this species occur in a range of biotopes. In contrast, little differences were observed among areas inhabited by *C. hotsoni*. Herein, according to the productivity hypothesis (MacArthur 1972), it is predicted that the more productive and diverse habitats with massy covers of different vegetation mainly on the north and northeastern Iran could support greater intraspecific differentiation for *C. elburzensis*. In contrast, lower intraspecific differentiation could be predicted for *C. hotsoni* living in the less productive hot and dry habitats in southeast of Iran with sparse vegetation cover. With regards to the greater intraspecific genetic distances reported for *C. elburzensis* as compared with *C. hotsoni* throughout Iran (Akbarirad et al. 2016a, 2016b), it would be assumed that geographical distances and the differences observed in some habitats of the first species may have influenced these genetic distances.

CONCLUSION

Species distribution models provide a better understanding of a species ecological niche and the present work provides useful knowledge on the areas of suitable environmental habitats where two related species of brush-tailed mice do and could occur. Such predictions could also identify localities for future field work and are also useful in following range shifts and changes in areas of contact in response to climate changes. Characterising the niche of these two species were based primarily on climatological and geological variables as well as plant coverage. However, other factors which may also be important in defining niche characteristics should be considered.

Herein, ecological distribution modelling of the two brush-tailed mice showed a low degree of niche similarities. However, further studies are needed in the case of character displacement and divergent niche evolution between *C. elburzensis* and *C. hotsoni*. Moreover, these ecological niche models identified areas in the north center of both South Khorasan and Kerman provinces suitable for these two species to co-occur. Studies on morphological and morphometric differences (especially in their contact zones), which are important to investigate character displacement for species identification associated with pre-mating isolation are suggested.

Finally, since dietary habits of sympatric or parapatric rodents partially determine their realised ecological niches, stomach content analysis will be helpful in defining rodents' trophic positions and the mechanism through which partitioning of niches and resources occurred; for example, using resources at different space or foraging of different food sizes.

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