

Microhabitat occupation and functional morphology of four species of sympatric agamid lizards in the Kyzylkum Desert, central Uzbekistan

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Abstract

Microhabitat occupation and functional morphology of four species of sympatric agamid lizards in the Kyzylkum Desert, central Uzbekistan.— We examined microhabitat occupation and functional morphology of four sympatric agamid lizards (*Phrynocephalus helioscopus helioscopus*, *P. interscapularis*, *P. mystaceus galli* and *Trapelus sanguinolentus*) at three sites in the arid zone of central Uzbekistan. At two sites located in sand dunes, substrate attributes played a key role in habitat selection by three syntopic species. At a third flat, stony site, *P. helioscopus* selected habitat non-randomly, tending to occur close to sparse, low vegetation. Syntopic taxa were separated in morphospace, and there was a trend for taxa with proportionally longer limbs to have faster field escape speeds. Field escape distances and predator avoidance tactics differed between species, with two main escape strategies (crypsis or sand-diving following an escape sprint). We caution that broad-scale threatening processes such as over-grazing and salinity may be having a detrimental effect on microhabitat features important to terrestrial reptiles in Uzbekistan.

Key words: Agamidae, Central Asia, Microhabitat occupation, Functional morphology.

Resumen

Ocupación del microhábitat y morfología funcional de cuatro especies de lagartos agámidos simpátridas del desierto de Kyzylkum, en Uzbekistán central.— Examinamos la ocupación del microhábitat y la morfología funcional de cuatro lagartos agámidos simpátridas (*Phrynocephalus helioscopus helioscopus*, *P. interscapularis*, *P. mystaceus galli* y *Trapelus sanguinolentus*) en tres localizaciones de la zona árida del Uzbekistán central. En dos localizaciones, situadas en una zona de dunas de arena, las características del sustrato tuvieron un papel clave en la selección del hábitat por parte de tres especies sintópicas. En una tercera zona, una llanura pedregosa, *P. helioscopus* no seleccionaba su hábitat al azar, con una clara tendencia a situarse cerca de vegetación baja y dispersa. Los taxa sintópicos estaban separados en el morfoespacio, y existía la tendencia entre los taxa con las extremidades proporcionalmente más largas a tener una mayor velocidad de huida. Las distancias de huida de campo y las tácticas de evitación de los depredadores diferían según las especies, con dos estrategias de huida principales (cripsis o enterramiento en la arena, seguidos de una carrera de escape). Hemos de advertir que los procesos amenazadores a gran escala, tales como el sobrepastoreo y la salinización pueden tener un efecto perjudicial sobre las características del microhábitat que son importantes para los reptiles terrestres de Uzbekistán.

Palabras clave: Agamidae, Asia central, Ocupación del microhábitat, Morfología funcional.

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Introduction

Central Asia, which encompasses the desert regions of Kazakhstan, Kyrgyzstan, Uzbekistan, Turkmenistan, has pronounced landscape heterogeneity, from high mountain ranges, to pebble, sand and steppe deserts. The deserts of Central Asia have some of the highest levels of biological richness of all the Eurasian deserts (Szczerebak, 2003). Despite this high biodiversity we still have limited understanding of the biogeography and ecology of the constituent reptile species, which show high levels of regional endemism. Qualitative descriptions of the general habitats of most of these taxa have been synthesised in field guides (Szczerebak, 2003; Ananjeva et al., 1998, 2006). However, very limited quantitative data exist on their microhabitat use (Bogdanov, 1960; Ananjeva & Tuniyev, 1992; Brushko, 1995), and few studies have investigated the functional link between morphology and microhabitat for lizards in this region (Sukhanov, 1974; Ananjeva, 2003).

Of the Central Asian countries, the Republic of Uzbekistan has a particularly diverse vertebrate fauna that includes approximately 60 reptile species. Uzbekistan is facing considerable natural resource management challenges. Extensive agricultural development and natural resource demands around highly populated areas have led to large-scale environmental problems such as desertification, water and soil pollution, and increased soil salinity (UNEP, 1999; UNDP, 2001). These processes have undoubtedly affected vital habitat attributes for numerous wildlife taxa. Detailed knowledge of the conservation status of wildlife in Central Asia is limited, and concern for the future of some reptiles in Uzbekistan is mounting (NBSAP, 1998). Sixteen reptile taxa have been listed by the International Union for Conservation of Nature and Natural Resources as threatened in The Red Data Book of Uzbekistan (2003; see also Ananjeva et al., 2006). Many lizard species in Central Asia occur in geographically restricted habitats such as desert dunes, and are considered habitat specialists (Szczerebak, 2003; Ananjeva et al., 2006). Quantification of microhabitat utilisation and functional morphology can provide important information for conservation strategies and management actions, by affording a greater understanding of an animal's ecological niche and resource requirements.

We present the first study to investigate microhabitat utilisation and functional morphology of Central Asian agamid lizards. To do this we quantify microhabitat use, escape speed and morphology, and discuss the functional link between escape behaviour and habitat, as has been undertaken for other reptile species (e.g., Irschick & Losos, 1999; Melville & Swain, 2000; Irschick & Garland, 2001). We studied four species that inhabit the Kyzylkum Desert in central Uzbekistan. These species included two sand substrate specialists (*Phrynocephalus interscapularis* and *P. mystaceus*) and two species that are not known to have specialised substrate preferences (*P. helioscopus* and *T. sanguinolentus*).

Numbers of *P. mystaceus* are in sharp decline, and there is serious concern regarding the conservation status of some populations of *P. helioscopus* (The Red Data Book of Uzbekistan, 2003). This study provides a greater understanding of habitat use by agamid lizards in this little-studied region, and provides a basis for future ecological, conservation and evolutionary studies.

Materials and methods

Site location and description

Sampling was conducted at three sites in the Kyzylkum Desert in central Uzbekistan. The first (41° 45' N, 64° 02' E) and second sites (41° 48' N, 64° 38' E, near the village of Tamdi) consisted of undulating sand dunes, whilst the third site (41° 43' N, 64° 28' E, also near Tamdi) consisted of flat topography and a gravel substrate. The region is characterised by a cold winter from December to February, and a hot, dry summer from June to August. Extremes of temperature are common during the peaks of these seasons. Annual precipitation in the Middle Asian deserts is extremely low (100–200 mm).

Study species

Phrynocephalus helioscopus helioscopus is a small (body length to 70 mm) agamid that inhabits hard earthy soils and, less commonly, the sands of semi-deserts. It emerges from winter hibernation in late February or early March, produces two or three clutches of 2–7 eggs each year, and reaches maturity at one year (Bogdanov, 1960; Brushko, 1995; Szczerebak, 2003).

Phrynocephalus interscapularis is a very small (body length to 42 mm) agamid that inhabits sandy deserts with sparse vegetation. In the Kyzylkum this species emerges from hibernation in the second half of March, produces single eggs four times a season, and reaches maturity by the end of the first year of life with a body length of around 37 mm (Bogdanov, 1960; Szczerebak, 2003).

Phrynocephalus mystaceus galli is a large (body length to 120 mm) agamid that inhabits sandy desert with sparse grass and shrubs. It is active from late March or early April until October, has two mating periods in a season, produces 1–4 eggs per clutch, and reaches maturity at two years (Szczerebak, 2003).

Trapelus sanguinolentus aralensis is a common, large (body length to 188 mm), semi-arboreal agamid that inhabits a variety of habitats, ranging from sandy, earthy and rocky deserts to mountain slopes up to 1,200 m above sea level, and river and canal banks. It shelters beneath stones and in rodent burrows. It emerges from hibernation between late February and early April and remains active until October. Two clutches of 4–18 eggs are produced each season, and maturity is attained at two years and a body length of 65–80 mm (Szczerebak, 2003).

Habitat variables

The data were recorded by walking throughout each field site from approximately 07.00 until 19.00 hours. This method ensured coverage of the entire range of structural and thermal microhabitats available. This was done over a 2-week period from April to May 2003, with approximately 4 days spent at each location. Data were only collected on sunny, warm days when lizards could be fully active.

At the time and place that each lizard was captured, we recorded eleven structural characteristics of the microhabitat: relative vertical position on dune [top (3); mid-dune (2); swale (1) and no dune (0)]; distance (cm) to the nearest vegetation; distance (cm) to the nearest shelter; height (cm) above ground that the lizard was perched; diameter of perch (cm); visual estimate of the percentage of shrub cover in a 3 m radius surrounding the lizard; visual estimate of the percentage of ground and grass cover in a 3 m radius surrounding the lizard; visual estimate of the percentage of litter cover in a 3 m radius surrounding the lizard; average shrub height (cm) in a 3 m radius surrounding the lizard; visual estimate of percentage rock cover in a 3 m radius surrounding the lizard; visual estimate of percentage gravel cover in a 3 m radius surrounding the lizard.

We could not evaluate interspecific differences in microhabitat occupation at the gravel site near Tamdi, as we captured only *P. helioscopus* and a single *T. sanguinolentus* at this location. Consequently, in order to determine whether these lizards were selecting microhabitats non-randomly, we plotted a randomly positioned grid of 50 x 100 m (encompassing the full range of microhabitats used by the lizards) and recorded microhabitat variables as we would for an actual lizard capture every 5 m within the grid (resulting in 55 data points). The grid data points were only recorded at times of the day when lizards were active, allowing comparable measurements of thermal conditions.

Morphology

Active lizards were caught by hand or with a noose-pole. Immediately upon capture the lizard's body temperature was measured to provide an estimation of active body temperatures of each species in its preferred habitat.

Each lizard's gender was determined and nine morphological measurements were recorded: 1. Snout-vent length (SVL); 2. Tail length (only individuals with intact tails were included); 3. Pelvis width (distance between hip joints on dorsal surfaces); 4. Humerus length (distance from shoulder to apex of elbow); 5. Antebrachium length (distance from elbow apex to center of wrist); 6. Forefoot length (distance from center of wrist to claw tip of longest toe, IV); 7. Femur length (distance from insertion of hindleg at pelvis to apex of knee); 8. Crus length (distance from apex of knee to heel); and 9. Hindfoot length (distance from heel to claw tip of longest toe, IV).

Escape speed

Average escape speed was used as a measure of the functional link between morphology and the microhabitat occupied by each species. Our measurement of escape speed is not intended as a proxy for maximum performance ability, but rather an estimate of escape speed in an ecologically natural setting. There have been numerous studies that have measured running and locomotion in natural settings (e.g., Irschick & Jayne, 1999; Irschick & Losos, 1999), including the video techniques that we employ. It has been found that substrate and slope can alter the speed and behaviour of lizards (Irschick & Garland, 2001). Thus, our field-based measurements provide an ecologically relevant estimate of escape speed in a species' natural environment.

At the time of release, the lizard was aligned with a line marked in the substrate, and the escape sprint was recorded on a Sony Digital video camera for later analysis. The distance the lizard ran was measured to the nearest centimetre. To reduce the possibility of displacement and provide an accurate estimate of escape speed in their microhabitat, lizards were released for videoing at the point where they were first observed.

To ensure differences in escape speed were not related to temperature, the body temperature of all lizards were measured prior to videoing. As all lizards had active body temperatures (range: 25.1–35.2°C; mean = 30.1; SE = 0.28), there was no relationship between the body temperature and speed of the lizard ($n = 48$, $r^2 = 0.03$, $P = 0.278$). Even when analysed within species there was no relationship between escape speed and body temperature (*Phrynocephalus helioscopus* $n = 14$, $r^2 = 0.03$, $P = 0.475$, *P. interscapularis* $n = 16$, $r^2 = 0.03$, $P = 0.538$, *P. mystaceus* $n = 9$, $r^2 = 0.03$, $P = 0.644$ and *Trapelus sanguinolentus* $n = 9$, $r^2 = 0.31$, $P = 0.118$).

Videoed escapes were analysed using Quicktime 4.1.2 software (Apple Computers Inc., Cupertino, California, USA). We determined the duration of all runs by counting the number of frames (30 frames.s⁻¹) elapsed between the beginning and end of the escape movement. Speed was measured in m.s⁻¹ for each escape.

Data analyses

Principal components analyses (PCA) were used to reduce the dimensionality of the morphological data (FACTOR procedure of SYSTAT). Prior to analysis, all morphological variables were log-transformed, and the effect of body size was removed from all measurements by using the residuals for each of the log-transformed variables regressed on logSVL. In each case the principal components (PCs) were extracted from a correlation matrix of the raw data. Principal components axes were named by the correlations of the original variables to the PC: correlations with absolute values greater than 0.5 were considered important (following Tabachnick & Fidell, 1989). Resultant PC axes were explored using analy-

Table 1. Gender, field body temperature, presence at each field site, general description of habitats in which each species occurs, escape distance and speed of agamid lizards from the Kyzylkum Desert, Uzbekistan: G M/F. Gender M/F; Bt. Body temperature [$^{\circ}\text{C}$, $\bar{x} \pm (\text{SE})$]; Fs. Field site number; Hc. Habitat category; Ghd. General habitat description; Med. Maximum escape distance [m, $\bar{x} \pm (\text{SE})$]; Es. Escape speed [$\text{m}\cdot\text{s}^{-1}$, $\bar{x} \pm (\text{SE})$]; ^aNote that two of the *T. sanguinolentus* presented here were not captured at the sites where habitat attributes were assessed, and were not included in habitat analyses.

Tabla 1. Género, temperatura corporal de campo, presencia en cada localización, descripción general de los hábitats en los que se encuentra cada especie, distancia de escape y velocidad de huida de los lagartos agámidos del desierto de Kyzylkum, Uzbekistán: G M/F. Género M/H; Bt. Temp. corporal [$^{\circ}\text{C}$, $\bar{x} \pm (\text{EE})$]; Fs. Número de localización; Hc. Categoría de habitat; Ghd. Descripción general del hábitat; Med. Distancia máxima de huida [m, $\bar{x} \pm (\text{EE})$]; Es. Velocidad de escape [$\text{m}\cdot\text{s}^{-1}$, $\bar{x} \pm (\text{EE})$]; ^a Nótese que dos de los *T. sanguinolentus* que aquí presentamos no fueron capturados en lugares en los que se habían valorado los atributos del hábitat, y no han sido incluidos en los análisis del hábitat.

Species	n	G M/F	Bt	Fs	Hc
			Ghd	Med	Es
<i>Phrynocephalus helioscopus</i>	14	3/11	33.1 (0.70) Flat gravel desert	3 0.94 (0.12)	Ground-dwelling 1.49 (0.13)
<i>Phrynocephalus interscapularis</i>	16	10/6	32.4 (0.65) Undulating sand dunes	1 1.46 (0.14)	Ground-dwelling 2.26 (0.16)
<i>Phrynocephalus mystaceus</i>	9	4/5	32.3 (0.87) Dune tops in undulating sand dunes	1, 2 6.23 (0.81)	Ground-dwelling 4.12 (0.29)
<i>Trapelus sanguinolentus</i> ^a	11	7/4	35.4 (0.79) All habitats except	1, 2, 3 3.69 (0.60) dune tops	Semi-arboreal 2.70 (0.31)

sis of variance (ANOVA) with multiple comparisons (Tukey's procedure) to determine whether there were interspecific differences in morphological and microhabitat variables.

For each taxon, field body temperature, escape distance and speed were compared using ANOVA with multiple comparisons (Tukey's procedure). Maximum escape distance was regressed against SVL, and escape speed was regressed against limb length (i.e. the sum of the three limb measures for fore- and hindlimbs) whilst controlling for body size (SVL) by using the residuals of the various leg length variables. We used SYSTAT Version 10.2 (SYSTAT Software Inc., Richmond, California, USA) for analyses.

For the available habitat variables at each site (range-standardised), we computed a matrix of pairwise Euclidean distances between data points. We employed non-metric multi-dimensional

scaling (NMDS) ordination in two dimensions, and plotted the resulting ordination diagram as a scatterplot. Subsequently, convex hulls were drawn around the groups of data points according to which species had been captured there (or whether they were random points, in the case of the gravel site). We then fitted linear vectors of the original habitat variables to the ordination space, displayed as arrows overlaid on the plot showing direction of steepest gradient in each habitat variable. Significant differences between habitat attributes of lizard sites and random sites were determined using an Analysis of Similarity (ANOSIM) test, with 1000 random permutations. NMDS and ANOSIM procedures were implemented in the R statistical programming environment (R Development Core Team, 2004), with the aid of the add-in libraries MASS (Venables & Ripley, 2002) and *vegan* (Oksanen, 2005).

Table 2. Summary statistics of the 11 structural microhabitat variables recorded for each species of agamid lizards from the Kyzylkum Desert, Uzbekistan ($\bar{x} \pm SE$): Pd. Position on dune (^a estimate of relative vertical position on dune: top (3), mid-dune (2), swale (1) and no dune (0)); Nv. Nearest vegetation (cm); Ns. Nearest shelter (cm); Ph. Perch height (cm); Pd. Perch diameter (cm); Sc. Shrub cover (%); Ggc. Ground/grass cover (%); Lc. Litter cover (%); Sh. Shrub height (cm); Rc. Rock cover (%); Gc. Gravel cover (%).

Tabla 2. Resumen estadístico de las 11 variables de microhábitats estructurales estudiadas para cada especie de lagarto agámido del desierto de Kyzylkum, Uzbekistán ($\bar{x} \pm EE$): Pd. Posición en la duna (^a Estimación de la posición vertical relativa en la duna: cima (3), mitad de la duna (2), parte baja (1) y sin duna (0)); Nv. Vegetación más cercana (cm); Ns. Refugio más cercano (cm); Ph. Altura de la percha (cm); Pd. Diámetro de la percha (cm); Sc. Cubierta arbustiva (%); Ggc. Suelo/cubierta herbácea (%); Lc. Cubierta de mantillo (%); Sh. Altura de los arbustos (cm); Rc. Suelo rocoso (%); Gc. Capa de grava (%).

Species

Species	n	Pd ^a	Nv	Ns	Ph	Pd
	Sc	Ggc	Lc	Sh	Rc	Gc
<i>Phrynocephalus helioscopus</i>						
	14	0.0 ± 0.0	30.7 ± 4.50	103.2 ± 23.05	0.0 ± 0.0	0.0 ± 0.0
	2.4 ± 0.49	6.4 ± 1.25	0.9 ± 0.28	36.4 ± 5.09	12.6 ± 3.52	24.3 ± 4.29
<i>Phrynocephalus interscapularis</i>						
	16	2.1 ± 0.23	94.7 ± 35.26	167.8 ± 38.64	0.0 ± 0.0	0.0 ± 0.0
	1.9 ± 0.26	1.8 ± 0.46	0.2 ± 0.11	75.0 ± 12.04	0.0 ± 0.0	0.0 ± 0.0
<i>Phrynocephalus mystaceus</i>						
	9	3.0 ± 0.0	124.4 ± 28.49	170.0 ± 30.64	0.0 ± 0.0	0.0 ± 0.0
	2.9 ± 0.54	0.3 ± 0.24	0.7 ± 0.29	102.2 ± 10.90	0.0 ± 0.0	0.0 ± 0.0
<i>Trapelus sanguinolentus</i> ^a						
	11	0.8 ± 0.30	51.8 ± 14.5	63.4 ± 18.8	9.1 ± 4.76	12.7 ± 7.15
	4.4 ± 0.72	6.0 ± 1.21	1.5 ± 0.25	70.9 ± 8.47	3.6 ± 2.68	8.9 ± 4.76

Results

Habitat selection

Mean field body temperatures ranged from 32.3°C (*P. mystaceus*) to 35.4°C (*T. sanguinolentus*) (table 1). An ANOVA of these temperatures indicated significant differences among species ($F_{3,46} = 3.49$, $P = 0.023$). *Trapelus sanguinolentus* had a significantly higher body temperature than *P. interscapularis* (Tukey's HSD *post hoc* test, $P = 0.025$). *Phrynocephalus* spp. had similar mean field body temperatures that were all slightly lower than *T. sanguinolentus* (table 1). Although the latter species is semi-arboreal (versus ground-dwelling for the *Phrynocephalus* spp.), all specimens that we measured were first encountered either on the ground or perched on small mounds of sand or gravel.

The summary statistics for the 11 structural microhabitat characteristics for each species are provided in table 2. At the two sand dune sites we recorded data for 16 *P. interscapularis*, nine *P. mystaceus* and eight *T. sanguinolentus*. Analysis

of Similarities indicated significant differences in the habitat features associated with each species (ANOSIM statistic: $R = 0.3371$, $P < 0.001$). At the two sand dune sites *P. interscapularis* and *P. mystaceus* were associated with low shrub heights, long distances to vegetation and shelter, and occurred towards the tops of dunes (fig. 1). However, *P. mystaceus* occurred in a much more restricted range of habitat associations than *P. interscapularis* (most notably, position on dune, where *P. mystaceus* was only found on dune tops, and *P. interscapularis* tended to occur mid-slope and in swales between dunes). The generalist species, *T. sanguinolentus*, was associated with a wide range of habitat factors, although it occurred closer to shelter and vegetation than the other species and was found in areas with more vegetation and rock cover.

For the gravel site, we recorded data for 14 *P. helioscopus*, one *T. sanguinolentus* and 55 random points. A NMDS ordination of these data is given in figure 2. The result of the ANOSIM indicates that there are significant differences between the habitat features

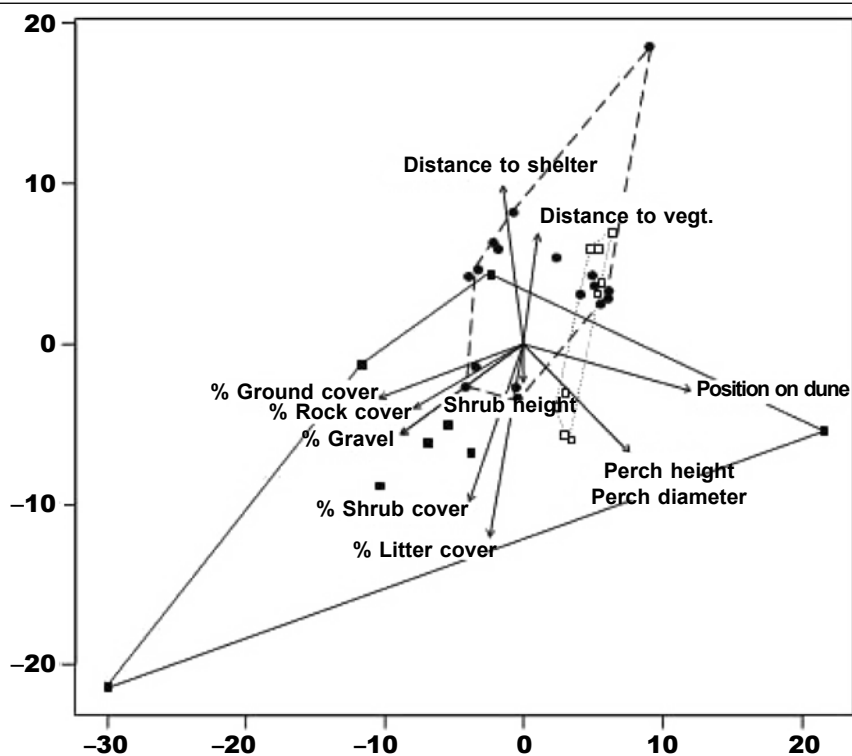


Fig. 1. Scatterplot of the non-metric multi-dimensional scaling ordination for species occurring at the sand dune sites, with arrows indicating the linear gradients of significant habitat factors. The stress of the ordination configuration is 0.088. Convex hulls have been drawn around data points of each species: *Trapelus sanguinolentus* (■, solid line); *Phrynocephalus interscapularis* (●, dashed line); and *Phrynocephalus mystaceus* (□, dotted line).

Fig. 1. Diagrama de dispersión de la ordenación ajustada multidimensional y no métrica de las especies que habitan en las localizaciones de las dunas arenosas; las flechas indican el gradiente lineal de los factores del hábitat significativos. El estrés de la configuración de ordenación es 0,088. Se han dibujado signos convexos alrededor de los puntos de los datos de cada especie: *Trapelus sanguinolentus* (■, línea continua); *Phrynocephalus interscapularis* (●, línea discontinua); y *Phrynocephalus mystaceus* (□, línea de puntos).

for each of these lizards and the random data points (ANOSIM statistic: $R = 0.2338$, $P = 0.007$). The vector plot indicates that *P. helioscopus* and the single *T. sanguinolentus* were associated with areas of higher vegetation cover than that typically found at random habitat points. *Phrynocephalus helioscopus* occurred in a much more restricted range of habitat associations than the randomly measured data points.

Functional morphology and escape speed

A summary of morphometric characters for each species is presented in table 3. Principal components analysis of the morphological variables revealed that limb proportions explained most of the variance in the data. This first axis (PC1) explained 42.8% of the variance in morphology. Lizards scoring high on

this axis had long limbs and hands / feet, and a wide pelvis. Lizards scoring low on this axis had short limbs (table 4). The second principal component axis (PC2) explained 17.5% of variance in morphology. Lizards scoring high on this axis had long tails and long upper hindlimbs, whilst lizards scoring low in this axis had short tails and upper hindlimbs (table 4). An ANOVA indicated a significant difference between species on PC1 ($F_{3,46} = 24.15$, $P < 0.001$) and a Tukey's HSD *post hoc* test showed that *P. mystaceus* scored significantly higher on this axis than the other three species (all P s < 0.001), and that *P. helioscopus* scored significantly higher than *P. interscapularis* ($P = 0.031$). Thus, *P. mystaceus* had longer limb proportions than the other species, relative to body size. An ANOVA of PC2 also indicated a significant difference between species ($F_{3,46} = 18.86$, $P < 0.001$). A Tukey's HSD *post hoc* test indicated that, on this axis, *T. sanguinolentus*

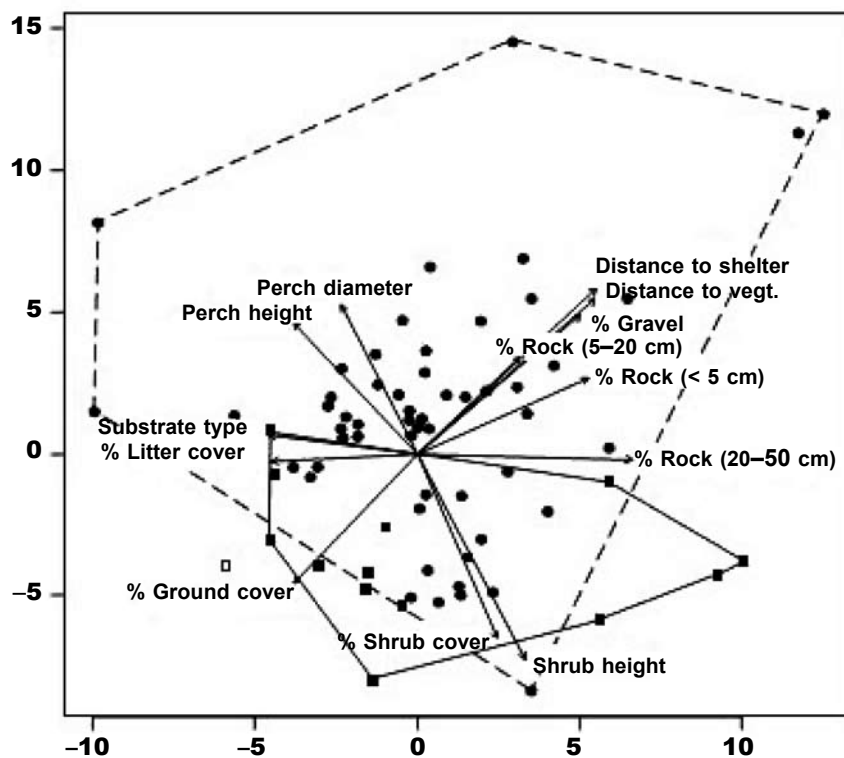


Fig. 2. Scatterplot of the non-metric multi-dimensional scaling ordination analysis for species occurring at the gravel site, with arrows indicating the linear gradients of significant habitat factors. The stress of the ordination configuration is 0.166. Convex hulls have been drawn around data points: *Phrynocephalus helioscopus* (■, solid line) and random habitat points (●, dashed line). A single *Trapelus sanguinolentus* was recorded at this site and is indicated by a single data point (□).

Fig. 2. Diagrama de dispersión del análisis de la ordenación ajustada multidimensional y no métrica de las especies que habitan en las localizaciones con suelo cubierto de grava; las flechas indican el gradiente lineal de los factores del hábitat significativos. El estrés de la configuración de ordenación es 0,166. Se han dibujado signos convexos alrededor de los puntos de los datos de cada especie: *Phrynocephalus helioscopus* (■, línea continua) y puntos del hábitat al azar (●, línea discontinua). Sólo se localizó un único *Trapelus sanguinolentus* en este hábitat, y ha sido consignado mediante un solo punto (□).

scored significantly higher than all of the other taxa ($P_s < 0.001$).

There was clear separation of these species in morphospace (fig. 3). The three species that were syntopic at the two dune sites, *P. mystaceus*, *P. interscapularis* and *T. sanguinolentus*, did not overlap in morphospace. Similarly, the two species occurring at the site with gravel substrate (*P. helioscopus* and *T. sanguinolentus*) did not overlap. Thus, even after the effects of body size were removed, there was morphological separation of all study species in limb proportions, pelvis dimensions and tail length.

The functional significance of each species' morphology in their respective habitat was quantified using escape speed and escape distance. Upon release, the two larger taxa, *P. mystaceus* and *T. sanguinolentus*, ran further than the other species (table 1; ANOVA of maximum escape distance, $F_{3,46} = 31.14$, $P < 0.001$).

After controlling for body size, *P. mystaceus* ran significantly further than all the other taxa (Tukey's HSD *post hoc* test, $P < 0.001$ for *P. helioscopus* and *P. interscapularis*, and $P = 0.001$ for *T. sanguinolentus*), and both *P. helioscopus* and *P. interscapularis* ran relatively further than *T. sanguinolentus* ($P < 0.001$ and $= 0.001$ respectively). Regression of maximum escape distance against SVL showed a significant positive relationship between longer-bodied taxa and escape distance ($F_{1,48} = 78.71$, $P < 0.001$). However, a similar test of distance versus combined fore- and hindlimb dimensions (controlled for body size) showed no significant relationship between leg length and escape distance ($F_{2,47} = 0.50$, $P = 0.610$).

The two larger taxa also displayed greater outright speed than the smaller species (table 1, ANOVA of escape speed, $F_{3,46} = 23.26$, $P < 0.001$). A Tukey's HSD *post hoc* test showed that, after controlling

Table 3. Summary of morphometric characters for each agamid species (mm, $\bar{x} \pm SE$): SVL. Snout-vent length; T. Tail; Pw. Pelvis width; Uf. Upper forelimb; Lf. Lower forelimb; HI. Hand length; Tf. Total forelimb; Uh. Upper hindlimb; Lh. Lower hindlimb; Fl. Foot length; Th. Total hindlimb; ^a Note that two of the *T. sanguinolentus* presented here were not captured at the sites where habitat attributes were assessed, and were not included in habitat analyses.

Tabla 3. Resumen de las características morfológicas de cada especie de agámido (mm, $\bar{x} \pm EE$): SVL. Longitud hocico–cola; T. Cola; Pw. Amplitud pélvica; Uf. Pata delantera superior; Lf. Pata delantera inferior; HI. Longitud de la mano; Tf. Longitud total de la pata delantera; Uh. Pata trasera superior; Lh. Pata trasera inferior; Fl. Longitud del pie; Th. Longitud total de la pata trasera; ^a Nótese que dos de los *T. sanguinolentus* que aquí presentamos no fueron capturados en lugares en los que se habían valorado los atributos del hábitat, y no han sido incluidos en los análisis del hábitat.

Species						
n	SVL		T	Pw	Uf	Lf
	HI	Tf	Uh	Lh	Fl	Th
<i>Phrynocephalus helioscopus</i>						
14	43.6 (1.66)		47.9 (1.80)	7.9 (0.33)	8.6 (0.26)	8.6 (0.54)
8.4 (0.21)	25.68 (0.92)		11.5 (0.38)	11.5 (0.38)	14.3 (0.38)	39.57 (1.14)
<i>Phrynocephalus interscapularis</i>						
16	31.1 (0.76)		33.0 (1.03)	4.7 (0.15)	5.7 (0.10)	5.2 (0.13)
5.8 (0.19)	16.63 (0.31)		8.6 (0.20)	10.3 (0.21)	12.3 (0.24)	31.22 (0.54)
<i>Phrynocephalus mystaceus</i>						
9	102.9 (2.58)		112.2 (2.01)	15.6 (0.38)	18.9 (0.66)	20.1 (0.51)
20.7 (0.66)	59.67 (1.26)		23.4 (0.69)	30.1 (0.61)	34.8 (0.83)	88.33 (1.70)
<i>Trapelus sanguinolentus</i> ^a						
11	94.5 (2.65)		156.4 (4.22)	12.0 (0.54)	16.8 (0.57)	16.9 (0.36)
15.1 (0.54)	48.82 (1.33)		21.6 (0.61)	27.2 (0.54)	27.4 (0.63)	76.18 (1.49)

for body size, *P. mystaceus* ran significantly faster than all the other taxa ($P < 0.001$), and that *P. helioscopus* was relatively faster than *P. interscapularis* ($P = 0.037$) and *T. sanguinolentus* ($P = 0.001$). Regression of escape speed against combined fore- and hindlimb measures (controlled for body size) was marginally non-significant ($F_{2,47} = 3.084$, $P = 0.055$), indicating a trend for species with proportionally longer limbs to have faster escape speeds. However, the interspecific relationship between escape speeds is confounded by the fact that species were escaping on different substrate types. Thus, rather than direct interspecific comparisons, these results should be interpreted as escape speed relevant to habitat occupation.

Discussion

Habitat selection

Thermal ecology plays an important role in habitat selection by agamid species (Izhaki & Haim, 1996; Melville & Schulte, 2001). The field body temperatures of agamids in the present study were within the range

recorded for arid-zone agamids from other continents (e.g. Greer, 1989; Melville & Schulte, 2001), but the mean body temperatures we recorded were slightly lower than those reported in these other studies. Other research on Central Asian agamid species found that *Phrynocephalus mystaceus* and *P. interscapularis* in the Karakum Desert were active at maximal body temperatures of 43–44 and 43.5–44°C respectively (Cherlin & Muzychenko, 1983). Melville & Schulte (2001) suggested that the field body temperatures they recorded for Australian arid-zone agamids were slightly lower than previously recorded for these taxa because they conducted their study in spring, when ambient and substrate temperatures are cooler than in summer. It is likely that the same situation applies to the present study; we conducted fieldwork in spring during relatively mild conditions, and it is plausible that the mean field body temperatures of the species that we studied may be higher later in the active season.

Our study species preferentially selected particular microhabitats. At each site a number of habitat characteristics were found to be important in distinguishing the habitats occupied by each species. For the three species occupying the two sand dune sites, *Phrynocephalus interscapularis*, *P. mystaceus* and *Trapelus*

Table 4. Principal components analysis (PCA) of lizard morphology. The eigenvalues, the proportion of the variance explained by the eigenvalue for each axis, and the loadings for the morphology variables are given.

Tabla 4. Análisis de componentes principales (PCA) de la morfología de los lagartos. Se dan los valores propios, la proporción de la varianza explicada por el valor propio para cada eje, y los pesos de las variables morfológicas.

	PCA	
	1	2
Eigenvalue	3.852	1.573
% of total variance explained	42.8	17.5
Cumulative % of total variance explained	42.8	60.3
	Loadings	
Snout–vent length	0.374	0.227
Tail residuals	–0.436	0.806
Pelvis residuals	0.640	–0.475
Upper hindlimb residuals	0.542	0.620
Lower hindlimb residuals	0.705	0.431
Foot residuals	0.778	–0.022
Upper forelimb residuals	0.683	0.173
Lower forelimb residuals	0.758	0.008
Hand residuals	0.823	–0.215

sanguinolentus, substrate played a significant role in microhabitat selection, whereas at the stony site near Tamdi the proximity of vegetation appeared to be the important factor for microhabitat selection for *P. helioscopus*.

The three species that occurred at the sand dune sites occupied different microhabitats. We found *P. mystaceus* only on dune tops, whereas *P. interscapularis* tended to occur mid–slope and in swales between dunes. In contrast, *T. sanguinolentus* tended towards habitat generalism at the sand dune sites, although it was never observed on the top of large dunes. Differential habitat use of swale versus dune tops has been recorded in studies of other desert lizard species. For example, in the Simpson Desert, Australia, differences have been found in the use of dunes tops, sides and swales between the agamid species *Ctenophorus isolepis* and *C. nuchalis* (Dickman et al., 1999). Similarly, in the White Sands National Monument, New Mexico, the iguanid species *Holbrookia maculata* and *Sceloporus undulatus* have also been found to select dune, hardpan or transitional substrates differentially (Hager, 2001). This latter study also found

that proximity to vegetation played an important role in microhabitat selection for these iguanid species.

At our third study site, which was stony and had patchily–distributed ground cover, the proximity of vegetation played an important role in microhabitat selection. We found that, compared to the random data points, *Phrynocephalus helioscopus* preferred stony microhabitats close to shrubs. However, this species has a large geographic range in Central Asia, occupying hard earthy soils and, infrequently, the sands of semideserts, so whilst our study site may be typical, further comparative study is warranted.

Functional morphology and escape speed

There were considerable differences in the relative morphology of the study species, most notably between *Trapelus sanguinolentus* and the three species of *Phrynocephalus*. We found relative tail length (PC2) to be significantly different between these two groups, where *T. sanguinolentus* had a relatively longer tail than the three species of *Phrynocephalus*. This difference may have a phylogenetic basis, which the current study is unable to address. The interspecific differences between PC1 (limb proportions) shows that *P. mystaceus* has significantly longer limbs than all of the other species. However, the remaining two species within the same genus (*P. interscapularis*, *P. helioscopus*) do not differ significantly in relative limb proportions to the more distantly related *T. sanguinolentus*, which indicates phylogenetic relatedness is not playing an important role. Thus, we are able to look at these traits in a functional framework.

Measuring escape speed in the field provides a direct and functional link between morphology and habitat use. Previous studies have shown that field escape speed is significantly less than the speed recorded in laboratory tests (e.g., Avery et al., 1987; Braña, 2003). A similar trend is likely for the species that we studied. The only direct previous measure of speed for any of our study species is for *P. mystaceus* (Sukhanov, 1974), where attempts to record speed both in the field and laboratory were largely unsuccessful, with only two brief speed cycles recorded in the laboratory. These speeds were 1.2 ms^{–1} for a cycle of about 0.09 seconds, and 1.8 ms^{–1} for 0.1 second (Sukhanov, 1974). The escape speeds we recorded in the field were comparable to those of two iguanid species studied in the laboratory that have similar habitat preferences and body shape to *P. mystaceus* (*Callisaurus draconoides* SVL = 76 mm, speed = 4.4 ms^{–1}; *Uma scoparia* SVL = 80 mm, speed = 4.0 ms^{–1}; Irschick & Jayne, 1998). However, these species have a smaller body size than *P. mystaceus* (SVL = 103 mm, speed = 4.12 ms^{–1}). This possible reduction in speed relative to body size in the field is unlikely to be due to temperature differences, as there was no correlation between body temperature and speed in the present study. However, it is likely that habitat plays a significant role in escape speed.

Locomotor performance is highly context–dependent, so that factors such as habitat selection can interpose filters that diminish potential per-

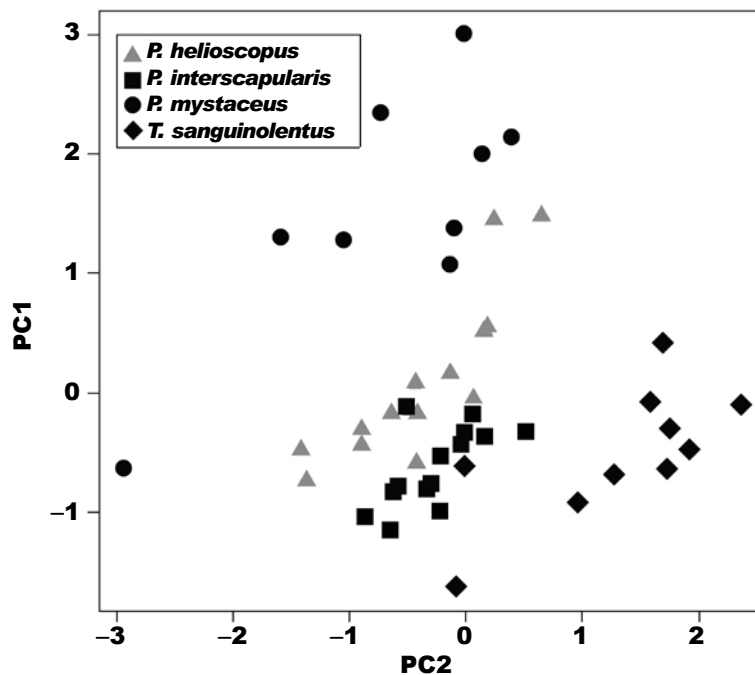


Fig. 3. The distribution of four study species along the first two morphological principal components axes.

Fig. 3. Distribución de las cuatro especies estudiadas a lo largo de los dos primeros ejes de componentes principales morfológicos.

formance (Braña, 2003; Irschick & Losos, 1999). In the loose sand habitats that *Phrynocephalus interscapularis* and *P. mystaceus* occupy, escape speed would be reduced due to an unstable and movable substrate that would dampen propulsive force, despite the possession by these species of specialised morphological features to assist in locomotion, such as toe fringes. Similarly, the habitat of *P. helioscopus* in the present study (stony valley with scattered ground cover) would also provide challenges to locomotor speeds. Thus, by measuring escape speed in the field we are able to directly examine the relationship between habitat occupation, morphology and locomotion.

The escape behaviour observed in a species, as well as its escape speed, can provide insight into habitat utilisation. A number of studies have found that there is a correlation between behaviour, morphology, performance ability and habitat use (e.g., Melville & Swain, 2000; Herrel et al., 2002). We found that escape distance varied significantly between the species. *Phrynocephalus interscapularis* and *P. helioscopus* escaped over very short distances, while *P. mystaceus* escaped over long distances. *Trapelus sanguinolentus*, on the other hand, had variable escape distances. This species occupied a wider range of habitats than the other species, was semi-arboreal, and was often observed perching

above or close to a burrow entrance. Consequently, *T. sanguinolentus* is likely to have a greater range of retreat options when fleeing predators, and often may not need to travel as far along the ground as the strictly terrestrial species.

Within the three *Phrynocephalus* species we observed two main escape behaviours: crypsis and sand-diving. Crypsis was used by *Phrynocephalus helioscopus*, which initially flee a short distance before freezing. This behaviour has been observed in other arid-zone species occupying stony plains, including the agamid *Tympanocryptis cephalus* and the iguanid *Phynosoma modestum* (Melville, pers. obs.). *Phrynocephalus mystaceus* and *P. interscapularis* used sand-diving when escaping. When approached, *P. mystaceus* would sprint away from the observer until it had just cleared the next rise, where they would rapidly bury themselves in the sand using lateral oscillatory movements. This sand-diving technique has previously been observed in members of this genus, and is known to be an adaptive trait in lizards occupying loose sand habitats (Arnold, 1995). Although *P. interscapularis* used a similar sand-diving strategy to avoid capture, it usually relied upon short bursts of sprinting and erratic changes of direction before eventually burying itself if pursuit continued. This sand-diving appeared to be a "last resort" strategy for this species.

Other studies of terrestrial lizards living in open, sparsely vegetated habitats have suggested that there are two possible behavioural escape strategies (Schulte et al., 2004): (1) running long distances at high speed to a potential shelter; or (2) remaining motionless and flattening the body against the ground. Whilst we observed both of these behaviours in *Phrynocephalus*, it is apparent from our observations that there may be a third and possibly intermediate category, where a species flees over short distances, using evasive techniques such as rapid changes in direction. Clearly there is scope for further comparative work on the agamid lizards of Uzbekistan.

Conservation

Studies such as this demonstrate the importance of microhabitat features for many small, terrestrial animals, particularly those with specialised habitat requirements. Many of these habitat attributes are vulnerable to threatening processes such as trampling by domestic stock, overgrazing, firewood collection, increasing salinity and desertification. The paucity of field research on vertebrate fauna in Central Asia means that there is little quantitative data with which to assess their current or former distribution, abundance or conservation status. Based on anecdotal accounts of declines in some taxa (Szczerebak, 2003), we suggest that there is an urgent need for surveys to determine the current geographic range of these species, and to establish programs to monitor the status of the species and their habitats. Such programs should address issues such as population trends over time, and the impact and mitigation of threatening processes.

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